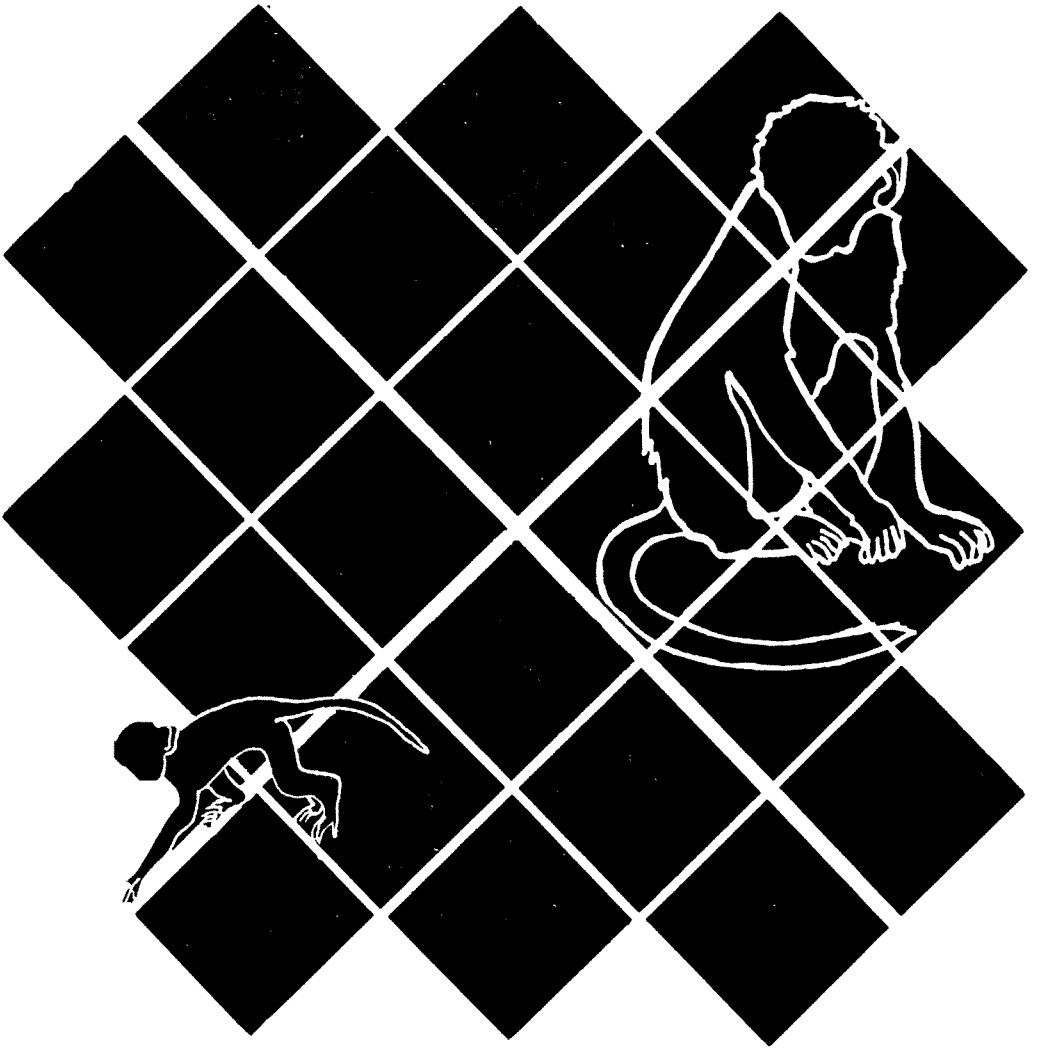

DEVELOPMENT OF EXPLORATORY BEHAVIOUR AND RANGE OF ACTION IN INFANT LONG-TAILED MACAQUES (*Macaca fascicularis*): EFFECTS OF RANGE OF ACTION OF THE MOTHER

Development of exploratory behaviour and range of action in infant longtailed macaques (*Macaca fascicularis*): effects of range of action of the mother

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Chapter 1

General Introduction

In this thesis a longitudinal study is presented concerning the question whether in long-tailed macaques the radius of action of the mother plays a role in the mother-infant relationship, and in the development of explorative behaviour and the range of action of her young. Special attention is paid to the question whether the radius of action of the mother has an effect on the development of phobic reactions to big novel objects of her young. In relation to this question, we tried to find out whether the kind of object and the age at which a young is confronted with a big novel object for the first time is of importance for its reactions to it. Some attention is paid to the effects of the absence of adults other than the mother on the development of explorative behaviour, on the development of the range of action, and on the reactions towards a big novel object.

For a long time research on phobias was dominated by theories in which conditioning is the mechanism behind the emergence of avoidance. These theories assume that a previously neutral stimulus (conditioned stimulus) acquires the capacity to elicit fear through association with a stimulus eliciting anxiety or pain (unconditioned stimulus). Ending exposure to this aversive stimulus by avoiding it, acts as a reinforcer. Consequently the conditioned stimulus will be avoided (see Marks, 1987a).

As it appeared that in humans some stimuli became an object of phobia more often than others, Seligman assumed that people are predisposed to associate fear more easily to certain stimuli (Seligman, 1971). In this theory so called "prepared stimuli" become more quickly associated with aversive stimuli than other stimuli. Preparedness is supposed to have evolved during the struggle for survival which favored those organisms that avoided stimuli that were a threat to life (Seligman, 1971; see also Eysenck, 1987; Marks, 1986; McNally, 1987; about influences of heredity on the development of fear).

Another variation on the conditioning theory concerns the acquisition of a phobia by observing someone undergoing an aversive experience. This so called "vicarious conditioning" (Bandura, 1969) implies that a subject that is watching someone acting fearfully to a particular stimulus consequently will avoid this stimulus.

Mineka, Cook and coworkers found that in Rhesus monkeys (*Macaca mulatta*)

vicarious conditioning as well as preparedness can play a role in the acquisition of a phobia. They showed that laboratory reared monkeys did not show fear of snakes till they saw a conspecific reacting fearfully to the presence of a snake. After this observation the laboratory monkeys also reacted fearfully to the snake (Cook et al., 1985; Mineka et al., 1984). Additionally observation of a conspecific reacting fearfully to a flower did not affect their behaviour towards the flower (Cook & Mineka, 1989; 1990).

In humans there are also phobias which cannot be ascribed to aversive experiences. It appeared that events like negative changes in the circumstances of someone's life (Solyom et al., 1974; cf Röder, 1990), abusive rearing experiences (Arrindell et al., 1983; De Ruiter & Van IJzendoorn, 1992), and anxious attachment (Bowlby, 1977) may have an effect on the development of a phobia (see also Marks, 1987b).

In humans it is very hard to demonstrate a causal connection between a phobia and these variables. In monkeys, however, there is evidence that rearing conditions may contribute to the development of a phobia. In a series of studies with long-tailed macaques (*Macaca fascicularis*) Röder (1990) compared two groups of monkeys in their reaction towards a big novel object. One group consisted of monkeys reared on surrogate mothers, the other group of monkeys reared by their own mothers in a harem. All monkeys were individually confronted with the same novel object at the ages of 6 and 15 months; at each age the object only differed in colour. A confrontation consisted of a series of 4 sessions of 30 min. each with intervals of 24 hr. The monkeys were individually tested on their reactions towards the object one month after a confrontation. The monkeys were tested once more at the age of 2 years.

Röder found that the rearing condition strongly affected the probability of development of phobic behaviour; most monkeys reared on surrogate mothers avoided the big novel object whereas young monkeys reared by their own mothers approached that object (see also Röder et al., 1989a,b; Timmermans et al., 1986). The colour of the object did not affect subjects' reaction.

Röder also studied the question whether the presence of the attachment figure (natural mother or surrogate mother) during the subject's first confrontation with the object had an effect on approach-avoidance behaviour. Although it is generally accepted that exploratory behaviour of young is enhanced by the presence of the mother, Röder et al. could not

confirm this in their experiment (Röder et al., 1989a). They found that monkeys confronted with a big novel object in the presence of the mother or the surrogate, did not explore the object more than monkeys confronted with the object in absence of the (surrogate) mother.

In another experiment Röder et al. found that approaching the object while clinging to their surrogate mothers or seeing their surrogate mothers approach the object, did not elicit approach behaviour in surrogate reared monkeys (Röder et al., 1989b).

The object that was used in these studies was a big paper bag filled with wood-chips that normally were used as bedding in the monkey cages. Throughout the years (up into adult age) the avoidance behaviour was persistent; even food offered near the bag did not elicit approach behaviour.

For two reasons this avoidance behaviour resembled a phobia: 1. the avoidance was very persistent, and 2. it was maladaptive (the bag was harmless and food offered near the bag was missed).

This animal model of phobic behaviour can not be explained by the models mentioned before. Explanation of this persistent avoidance by the conditioning model as well as an explanation based on the preparedness theory could be excluded since none of the monkeys ever had a negative experience with the bag. The third possible explanation, namely vicarious conditioning, also could be eliminated since in the experiments of Röder et al. (1989a) monkeys were individually exposed to the bag.

As studies in humans have shown that phobias may develop without conditioning (McNally & Steketee, 1985; Williams, 1987) the present animal model could be useful for the study of the acquisition of phobias without conditioning.

The following up study, presented in this thesis, deals with three questions concerning the development of exploratory and phobic behaviour:

-1-Is the avoidance behaviour of the phobic monkeys restricted to the bag?

-2-Does mobility of the mother play a part in the development of exploratory and phobic behaviour?

-3-Does the absence of adults other than the mother play a part in the development of exploratory and phobic behaviour?

(1) Röder et al. (1989 a,b) confronted and tested monkeys only with the paper bag; the assumption being that bag-avoidance was a simple phobia. That interpretation was based upon the fact that in a previous study there was no difference between monkeys of both rearing conditions with regard to their reactions to other novel objects (Timmermans et al., 1986). However, avoidance of one particular object and approach of other objects were not in accordance with reports of other investigators (Barnett & Cowan, 1976; Suomi, 1986) who reported avoidance behaviour with respect to various objects of the same class. For this reason monkeys that formerly were confronted and tested with the paper bag by Röder, were retested with other big novel objects. As size is a prepotent determinant of responses to novel objects (Menzel 1962), the monkeys also were tested with small novel objects.

(2) Röder (1990) concluded that rearing condition was a crucial factor in the development of phobic behaviour. The question raised now is which of the numerous differences between mother-rearing and surrogate-rearing were responsible for the differences in the youngs' reactions to the bag. There are some obvious differences between mother-rearing and surrogate-rearing. First of all, surrogate-reared monkeys are deprived of maternal care whereas mother-reared monkeys obviously are not. Whereas a surrogate mother is an inanimate object that offers the infant the opportunity to hold on to and to keep itself warm, a real mother adds activity and reactivity to these features. A mother manipulates her infant by restricting it and at a later age by rejecting and avoiding it. Another feature of a real mother is that she moves around through the environment with her infant and from birth onwards confronts the infant with physical as well as with social aspects of the environment while she is nearby. It is commonly accepted that the mother is serving as a secure base from which the infant more and more ventures away when becoming older (see Baldwin & Baldwin, 1978; Bowlby, 1977; Bronson, 1968; King, 1966; Suomi, 1984). In contrast to this, infants that grow up with static surrogate mothers have to explore and master the environment without their surrogate-mothers nearby. By moving about in the environment a real mother brings her infant into contact with various stimuli in the proximity of a secure base. Lack of this opportunity, as is the case in static surrogate-mothers, may have an effect on the development of exploratory behaviour and

consequently, on behaviour towards big novel objects.

In order to find out whether exploring the environment without maternal proximity influences the development of approach - avoidance behaviour with respect to a big novel object, we decided to limit the mother in her radius of action to a small part of the environment. In this way it was prevented that the mothers could support their infants in exploring the environment. This was done by restraining some mothers of a harem group to a small part of the cage they lived in and offering their infants the opportunity to leave this restricted area and enter the whole harem cage.
In the harem cage, in which the restrained mothers and their infants were housed, other mothers with their young could move around freely. These infants were the control group. Infants reared by restrained mothers and infants reared by unrestrained mothers were compared in their reactions towards a big novel object.

It is generally assumed that during a very early phase in the development of an infant novelty does not evoke fear whereas in the following phase novelty evokes avoidance behaviour. During this phase the presence of the mother can reduce these fear reactions (Bronson, 1968). As the infant grows older, it develops the capability to cope with novelty independently. In Röder's study infants were individually confronted with a big novel object in a phase in which it is assumed that the mother is needed for fear reduction. If the age of the subject at which the first individual confrontation with a novel object took place determines the reaction of the subject towards that object, it is important to know what the effects are of the age at which subjects are confronted with a novel object for the first time. Therefore, subjects were confronted with a novel object at an age they are assumed to be dependent on their mothers' presence in order to explore novelty, and at an later age, at which they are assumed to be able to explore novelty independently, they were confronted with an other novel object.

(3) Röder compared young reared with surrogates in a peer group with young reared by their mothers in a harem group. So, besides the difference in the attachment figures there was a difference with respect to the social environment. To study whether (sub-)adult conspecifics other than the mother have an effect on the development of

explorative behaviour of infant monkeys a third group was used in which infants grew up together with restrained mothers but without other free moving adult conspecifics. As in the harem, infants were given the opportunity to leave the restricted area and enter the whole cage.

By restraining the mothers we may influence maternal behaviour of these mothers and also influence the behavioural development and the development of the range of action of their infants.

Besides the effects of restraining the mother on the development of exploratory and phobic behaviour of her infant, this thesis deals with the questions whether restraining the mother:

-Has an effect on mother-infant relationship?

-Has an effect on the development of behaviour and range of action of their infants?

Restraining the mother may evoke an increase of rejecting and avoiding behaviour towards her infant (Castell & Wilson, 1971; Kaplan, 1972; Wolfheim et al., 1970). According to Kaplan (1972) the increase of punishing and avoiding behaviour of the mothers is considered to be a reaction to their infants' attempts to make contact. In the studies of Castell & Wilson (1971), Kaplan (1972), and Wolfheim et al. (1970) mother and infant were socially isolated and enclosed in a small cage. In our setup mother and infant were not socially isolated and infants had the opportunity to leave their mothers' cage. However, in our setup restrained mothers also did not have the opportunity to keep a greater distance from their infants than the cage allowed them, so infants did have the opportunity to contact their mothers frequently. As a consequence, these mothers may show more avoiding and rejecting behaviour than mothers having the opportunity to keep a distance from their infants. Apart from the lack of opportunity to keep distance from their infants, restrained mothers also could not follow their infants when they left the cage in which their mothers were housed. Because of this, restrained mothers may as well try to keep their infants inside their cages by restricting them.

Comparison of restrained and unrestrained mothers in their relationships with their infants may answer the question whether restraining the mother has an effect on mother-infant

relationships.

Normally during the first months the mother accompanies her infant when it reconnoitres the environment. In this way the proximity of the mother, as a secure base, promotes the development of explorative behaviour (e.g. Baldwin & Baldwin, 1978; Bronson, 1968; King, 1966). Infants of restrained mothers have to explore the environment without this maternal support. Therefore, the development of explorative behaviour of her infant can be influenced by restraining the mother.

According to Hinde & Spencer-Booth (1968), and Berman (1980) infants take the initiative in leaving their mothers during the first 2-3 months of life; in that period mothers follow their infants. Later, these roles are reversed.

As infants get familiar with the environment within proximity of the mother, it is questionable whether infants of restrained mothers do leave their mothers to enter an unfamiliar environment. Therefore infants of restrained mothers may develop a limited range of action.

By comparing infants of unrestrained mothers with infants of restrained mothers within a harem an answer can be found to the question what the effects are of a restrained mother on the behavioural development and the development of range of action of her infant.

Comparing the behavioural development and the development of range of action of infants growing up with restrained mothers but without the presence of other adults with the development of infants growing up with restrained mothers within a harem can give us an impression of the effects of the presence of adults other than the mother on infant's development.

This thesis is organized as follows. The **second chapter** bears on the question whether we are dealing with a simple phobia or not. Surrogate-reared and mother-reared monkeys, of which it was known that they formerly avoided or approached the bag, were tested to assess their approach-avoidance behaviour with respect to two other big novel objects and four small novel objects. The **third chapter** focusses on the question whether restraining mothers has an effect on mother-infant relationships. Therefore, during the first 6 months of the infant's life, restrained and unrestrained mothers and their infants, that were housed in a harem cage, were compared in their behaviours concerning their

relationships. The **fourth chapter** describes the effects of restraining mothers on the development of behaviour and range of action of their infants. In order to find out what the effects are of having a restrained mother, infants of restrained and infants of unrestrained mothers were observed for one year, and compared in their behavioural development and the development of range of action. The **fifth chapter** deals with the question whether growing up with a restrained mother has an effect on the approach-avoidance behaviour with respect to big novel objects. Therefore, at the age of 6 months the infant monkeys were confronted with a big novel object for the first time. Between the age of 7 and 24 months the infants were tested on approach-avoidance behaviour with respect to that object four times: at the ages of 7, 12, 18 and 24 months. To answer the question whether the development of persistent avoidance of a big novel object depends on the age of first exposure, the infants were confronted with a second big novel object at the age of 20 months. At that age infant long-tailed macaques are assumed to explore novel objects and situations independently. The approach-avoidance behaviour with respect to this second object was tested at the ages of 21 and 26 months. The **sixth chapter** goes into the question whether the absence of (sub-) adults has an effect on infants. Here the development of explorative behaviour, the development of the range of action, and the reactions towards a big novel object in subjects that grew up with mothers that were restrained in their radius of action to a small part of a cage is described. Except subjects and their mothers no other monkeys were present. So, outside the mothers' cages infants only had age-mates. This rearing condition only differs from surrogate rearing with regards to the type of attachment figure. It also differs in one aspect from the harem condition, namely in the absence of adults outside the mothers' separation cages. In the **seventh chapter** the results of all experiments are discussed.

Summary of observations and tests.

AGE	OBSERVATIONS
week 4 till week 26	Mother-Infant relationships
week 6 till week 52	Development of infant's behaviour and radius of action
week 26	Confrontation with the first big novel object
week 30	First test on approach-avoidance behaviour with the first object
week 52	Second test on approach-avoidance behaviour with the first object
week 78	Third test on approach-avoidance behaviour with the first object
week 86	Confrontation with the second big novel object
week 90	First test on approach-avoidance behaviour with the second object
week 104	Fourth test on approach-avoidance behaviour with the first object
week 112	Second test on approach-avoidance behaviour with the second object

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Chapter 2

Responses to Novelty in Phobic and Non-Phobic Cynomolgus Monkeys: The Role of Subject Characteristics and Object Features

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Abstract. In two previous studies it has been shown that most surrogate-reared cynomolgus monkeys became phobic of a harmless object (a big paper bag) while most mother-reared monkeys approached that object Results of the first study seemed to indicate that the phobic reaction was restricted to the bag Barnett and Cowan (*Interdisciplinary Science Review*, 1, 43-62, 1976) and Suomi (*Anxiety disorder in childhood*, pp. 1-23, 1986), however, reported that subjects (respectively rats and monkeys) that avoided a first novel object also avoided subsequent novel objects. In the present study we exposed phobic (bag-avoiding) and non-phobic (bag-approaching) monkeys from the study by Röder, Tummermans and Vossen (*Behaviour Research and Therapy*, 27, 221-231, 1989) to several big and small novel objects. Our results show that, irrespective of their rearing conditions, subjects that were phobic also avoided big novel objects while subjects that were non-phobic approached big novel objects. The reaction to small novel objects was independent of the previous reaction to the bag

Introduction

Novelty can evoke competition between on one hand the tendency to approach and on the other hand the tendency to avoid an object or situation. This state has been called approach-avoidance conflict (Russell, 1973; Corey, 1978). The reaction of a *S* to novelty is primarily depending on the age of the *S*, the characteristics of the novel stimuli and the nature of previous experiences of the *S* (e.g. Birke & Archer, 1983; Cowan, 1983). Among the previous experiences of the *S* certain kinds and amount of environmental stimulation during early youth profoundly affect later exploratory behaviour (Corey, 1978; Stevenson, 1983). Several investigators reported abnormal fear and avoidance reactions in animals reared under conditions of environmental restriction when a novel object was presented to these animals. Rats, for instance, which were reared in a restricted environment or in social isolation avoided novel objects and novel situations (resp. Hughes, 1971; Joseph & Callagher, 1980; Widman & Rosellini, 1990; and Turpin, 1977). Also monkeys reared in a restricted environment or under conditions of social deprivation showed restrained behaviour towards novel objects and novel situations (resp. Menzel, Davenport & Rogers, 1963a, b; Menzel, 1962; Elias & Samonds, 1973; Sackett, 1972).

In a longitudinal study Timmermans and co-workers found a very persistent type of avoidance behaviour in monkeys (*Macaca fascicularis*) caused by mother deprivation. Monkeys reared in a peer group on surrogate mothers avoided a harmless novel object (a big paper bag) while monkeys reared by their mothers in a breeding group approached that same object (Timmermans, Röder & Hunting, 1986). Avoidance as well as approach of the

bag persisted from the age of 1 yr up and into adulthood. The authors reported that this avoidance was object-specific; behaviour evoked by other novel objects (rat, cat, plastic doll and metal box) was the same in both groups of monkeys.

This object-specificity of avoidance of novelty, however, was not found by other investigators. Barnett and Cowan (1976) and Cowan (1983) reported that if rats avoided a first object they also avoided other novel objects. The authors concluded that in general rats are either avoiders or non-avoiders. This individual characteristic has also been found in monkeys. Monkeys that as infants avoided a particular novel object also as adults showed avoidance reactions to other novel objects belonging to the same class (Suomi, 1986).

Röder et al. (1989) replicated the experiment of Timmermans et al. (1986) and again found that most monkeys reared in a peer group on surrogate mothers avoided the paper bag previously used by Timmermans et al. This time, however, a few surrogate-reared *Ss* did not avoid and a few mother-reared *Ss* did avoid the object. The presence of these four classes of monkeys, surrogate- as well as mother-reared avoiders and non-avoiders, offered the opportunity to collect new data concerning the discrepancy between the findings of Barnett, Cowan and Suomi on one hand and Timmermans on the other.

In the present study it was investigated whether the avoidance reaction to the big paper bag shown by the monkeys in the study by Röder et al. (1989) was restricted to that object. Monkeys that were known persistently to avoid as well as monkeys that were known persistently to approach the bag were confronted with two big novel objects. As size is a prepotent determinant of responses to novel objects (Menzel, 1962) the same monkeys were also confronted with several small novel objects in an additional experiment.

Materials and Methods: General

Subjects

Male and female Cynomolgus monkeys were used as *Ss*. They were born and raised under laboratory conditions. A number of these monkeys was separated from their

mothers within 1 week after birth and reared on surrogate mothers in a peer group (surrogate-reared; SR). The others grew up with their mothers in a breeding group consisting of a number of adult females, one adult male and a number of young (mother-reared; MR). The *S*s had been used before in another experiment (see Röder et al., 1989). In Röder's experiment they were individually tested with a novel object (a big paper bag) at the ages of 7, 9 and 16 months. The results of these tests showed that 82% of the SR and 25% of the MR monkeys persistently avoided the bag. The other monkeys approached the bag and took the pieces of apple lying near it.

Housing

At the time of the present experiments all monkeys lived in heterosexual groups housed in separate rooms in cages measuring 4.0 x 3.6 x 2.0 m. Each cage was divided into two compartments of equal size by an opaque partition with a passage that was closed with a sliding door during testing of individual monkeys. The right compartment contained the experimental setup which was familiar to the monkeys as it was a part of their home cage. For details of housing and experimental setup the reader is referred to Röder et al. (1989). The floor of the cage was covered with wood chips which were refreshed bimonthly. All cages were fitted with vertical and horizontal climbing-poles. Water was available ad libitum and food (Hope Farms monkey chow) was given twice a day. Weekly the monkeys got pieces of apple and cereals. The lights were on from 8.00 a.m. till 8.00 p.m.

Procedure

All monkeys were tested individually. Depending on the kind of test five pieces of apple or the object together with five pieces of apple were fixed on the flap of the presentation box and the box was closed. Half an hour before testing a *S* was put into the right compartment which contained the experimental setup and the passage between the compartments was closed. The rest of the group stayed in the left compartment. The *S* was then put into the so-called start cage and offered two pieces of apple. This was done to determine whether apple was an attractive stimulus for *S*s which were separated from their cage mates. After the experimenter had left the cage, the flap of the box was lowered and

the test was started by opening the start cage. The position of the presentation box was such that the monkey could reach the flap with the object and the pieces of apple on it from the floor only. The behaviour of the *S* was recorded for 30 min. Then the presentation box was closed and the *S* was reunited with the group by opening the passage in the partition. The test procedure was the same in both experiments and for all objects.

Parameters

During the tests the monkeys were observed by means of remotely controlled video equipment. The behaviour of the *S* and its location in the test compartment were registered with an event recorder (More Observational Systems). The following parameters were scored:

Time on floor; the time spent on the floor outside the start cage

Time near object; the time spent on the floor area within 0.5 m of the object

Locomotion; the time spent on locomotion

Autoactivity; the time spent on grooming, scratching and thumb-sucking

Latency till the first piece of apple was taken

Number of pieces of apple taken

1. Tests with Big Novel Objects

Objects

The objects to be used in this experiment had to meet a number of requirements. Because size is an important determinant of responses to novel objects, the size of the novel objects should equal that of the bag used in the preceding experiment. The bag was a blue creasy paper bag filled with wood chips. Because the objects should be novel their shape and surface should differ from the bag. The first novel object we used had a triangular shape and was made of polystyrene covered with brown jute. The second novel object was a wooden chairlike construction painted blue (see Fig. 1).

Procedure

The experiment consisted of three blocks of tests. Each block of tests with objects

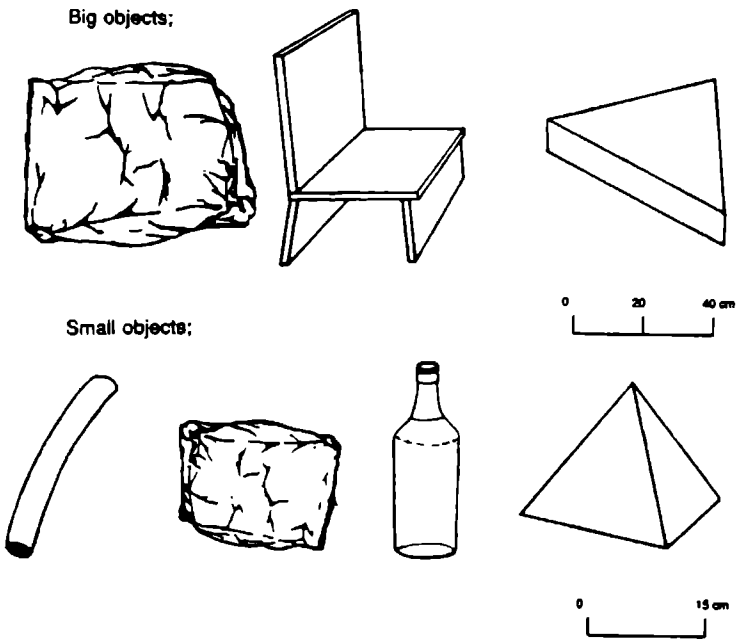

Fig. 1. *Objects used in the experiments.*

was preceded by a so-called apple test in which pieces of apple were presented, but no object, in order to assess whether the monkeys would take pieces of apple at the place where the object would be presented.

In block I 12 MR monkeys (8 males and 4 females) and 11 SR monkeys (6 males and 5 females) were tested to compare their approach-avoidance behaviour with respect to the bag and the triangle. The average age of the *Ss* at that time amounted 31 months, ranging from 20 to 36 months. The objects were presented to each individual monkey in seven sessions of 30 min each, with intervals of at least 24 or at most 72 h. In the first two sessions the monkeys were tested with the paper bag to establish their reactions to this object at this age. In the next five sessions they were alternately confronted with the triangle and the bag. So the object sequence was: bag, bag, triangle, bag, triangle, bag, triangle.

In block II, 15 months later at a mean age of 42 months, five MR monkeys (2 males and 3 females) and five SR monkeys (all females) were again tested with the bag in four sessions of 30 min with intervals of 24 h (the other 13 monkeys no longer were available). Six weeks later, in block III, the same *Ss* were tested with the chair, in four sessions of 30 min with intervals of 24 h.

2. Tests with Small Novel Objects

Four months after the last test with a big object when the monkeys had an average age of 46 months the tests with small objects began.

Objects

The objects used in this experiment should be distinctly smaller than the objects used in the previous experiments. We chose three objects that differed in shape, colour and surface texture from the big ones used before, and, a small copy of the blue paper bag. The small bag was used to find out whether generalization would occur from the big bag to a small one. The volumes of these four objects amounted only 5% of the volume of the paper bag used before. The objects were (see Fig. 1): a yellow wooden pyramid, a brown glass bottle, a piece of yellow and black garden hose, and a small blue paper bag.

Procedure

The same 10 *Ss* as in the last two blocks of the previous experiments were used. The monkeys were tested in sessions of 30 min, 1 per day on 4 successive days, on each of which one of the objects was presented. The order in which the objects were presented was different for each of the animals. Contrary to the preceding experiments the *Ss* were not tested with the big paper bag this time because the last test took place only 4 months ago and the reactions had been quite stable at all preceding tests in the course of almost 4 yr. The test procedure and the behavioural parameters were the same as used in the previous experiment.

Results

1. **Big Objects**

Test block I, bag and triangle, age class 31 months

All monkeys ate pieces of apple when they sat in the start cage separated from their cage mates and also in the apple tests preceding the tests with an object. So apple was an appropriate appetitive stimulus to be offered together with novel objects in individual test sessions.

In Table 1 the approach-avoidance behaviour (taking or not taking pieces of apple) of each monkey towards big and small objects is shown. The results of the test with the

Table 1. *Individual performance (taking apple) in presence of various objects.*

	Rearing	mother reared												surrogate reared										
	Monkey	BM	TJ	MC	JR	TN	SN	TW	JB	HA	HU	MA	BR	CH	BA	PI	TE	MI	KN	NO	TR	VI	JO	KS
Age (months)	Objects																							
	large																							
31	bag	+	-	+	+	+	+	-		+	+	+	±	-	+	-	-	+		-	+	-	-	-
	triangle	+	-	+	+	+	+	-	-	+	+	+	-		+	-	-	+	-	-	+	-	-	-
42	bag	+				+				+	+		-	-				+		-	-	-		
	chair	+				-				+	+		-					+		-	+	-		
46	*small*																							
	pyramide	-				+				+	+		+	-				+		+	+	+		
	garden-hose	+				+				+	+		+	+				+		+	+	+		
	bottle	+				+				+	+		+	+				+		+	+	+		
	bag	+				-				+	+		+	-				+		+	+	+		

\+ =more than one piece of apple has been taken
\- =no apple has been taken
± =only one piece of apple has been taken

triangle clearly show that avoidance is not restricted to the bag. Further it is quite clear that monkeys which avoided the bag, avoided the triangle as well. Only one *S*, called BR, disobeyed this rule, but BR took only one piece of apple in tests with the bag. Data from previous experiments (Röder et al., 1989) show that BR never took a piece of apple in tests with the bag then.

Röder et al., called a monkey phobic if it had never taken a piece of apple near the bag at the end of a series of tests closing at the age of 16 months, and non-phobic if *S* at that time had taken several pieces. When we adopt this classification for our present data then we can state the rule that (BR excepted) phobic monkeys avoided the triangle and non-phobic ones approached it no matter whether their rearing condition had been 'mother' or 'surrogate mother'.

The contingency coefficient, taken as a measure of the association between behaviour towards the triangle (approach or avoidance) and rearing condition (mother or surrogate), amounts 0.37, whereas this measure amounts 0.68, for the association between behaviour towards the bag (approach or avoidance) and behaviour towards the triangle (approach or avoidance). So previous behaviour towards a big object appeared to be a better predictor for ensuing behaviour towards a big novel object than rearing condition.

In Fig. 2 the latencies till the first piece of apple was taken and the time spent near the object (within 0.5 m) are shown. Neither in phobics nor in non-phobics there were differences in the latencies till the first piece was taken and the time spent near the object between the bag and the triangle (Wilcoxon matched-pairs test). Latencies in phobics were significantly longer than in non-phobics (bag, $p < 0.001$; triangle, $p < 0.01$, Mann-Whitney U test). The time spent near the objects was significantly longer in non-phobics than in phobics (bag, $p < 0.01$; triangle, $p < 0.001$, Mann-Whitney U test).

Test blocks II and III, bag and chair, age class 42 months

Comparison of the behaviour evoked by the bag and the chair in a sample (n=10) of the Ss used in the preceding experiment produced essentially the same results as the comparison of the bag with the triangle. Monkey TN disobeyed the rule that non-phobics approached novel objects by taking pieces of apple near the bag, as usual, but not near the chair, although he before took apple near the triangle. Monkey TR did not take pieces of

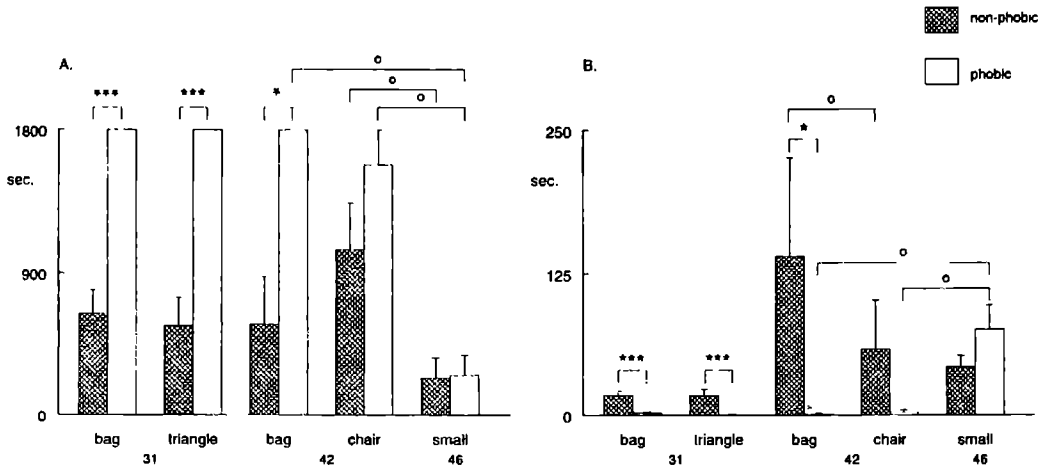

Fig. 2. *Mean latency till first piece of apple was taken (A) and mean time spent near various objects (B) by phobic and non-phobic monkeys. n=12 (non-phobic), 11 (phobic at 31 months; n=5 (phobic), 5 (non-phobic) at 42 and 46 months.*
****P < 0.001, *P< 0.05, (Mann-Whitney U test); O P= 0.0591 (Wilcoxon matched pairs test)*

apple near the bag this time. At the age of 16 months this monkey was found phobic, but after modelling at the age of 24 months it took pieces of apple near the bag (Röder et al., 1989).

The latencies before taking the first piece of apple also were in accordance with the outcome of the tests with the triangle. The only difference was that this time phobics and non-phobics did not differ in latency before the first piece of apple was taken in the test with the novel object (chair).

Phobics spent less time near the bag and the chair than non-phobics but this difference was significant only in case of the bag (bag, $p < 0.05$; chair, $0.05 < p < 0.10$; Mann-Whitney U test). Further, the discrepancy in time spent near the bag and the chair by non-phobics was not significant ($p = 0.0591$); Wilcoxon matched-pairs test).

2. **Small objects**

Age class 46 months

The presentation of small novel objects at the age of 46 months produced quite different results. Almost every monkey took pieces of apple near each of the objects. The ratio approach:avoidance was not 50:50, as it was with the big novel objects, but, 36:4 when all 40 sessions with small objects are lumped. The small bag was not avoided more often than the other small objects. Phobics and non-phobics did not differ in the number of pieces of apple taken. Seven out of ten monkeys took apple near each small object, one non-phobic avoided the pyramid, one other non-phobic avoided the small bag, and, one phobic avoided the pyramid and the small bag. A relation of approach-avoidance behaviour with rearing conditions was not found.

In phobics as well as in non-phobics there was a discrepancy between the reactions to small objects and those to the chair that, although not significant, seems worth mentioning: latencies before the first piece of apple was taken near the small objects were shorter than with the big novel object (chair) (p =0.0591, Wilcoxon matched-pairs test).

Phobics and non-phobics did not differ in their latencies till the first piece of apple was taken and the time spent near the small objects.

As for the other parameters (time on floor, locomotion, and autoactivity) there were few differences. Non-phobics spent more time on the floor than phobic (p <0.05, Mann-Whitney U test) with both big objects (bag and triangle) during the first block of tests. Phobics showed more autoactivity than non-phobics (p <0.05, Mann-Whitney U test) during the second test with the big bag (age 42 months) and during the tests with the small objects (p <0.05, Mann-Whitney U test). The parameter locomotion did not differentiated in any test.

Discussion

Cynomolgus monkeys that had avoided a big paper bag during tests taken in the age period from 7 till 16 months (see Röder et al., 1989) still avoided this object at the

ages of about 31 and 42 months. Monkeys that had not avoided the object in the earlier tests still approached it during tests in the present study. The persistency of the reactions to this object agrees very well with findings from a previous study (Timmermans et al., 1986).

With respect to the reaction to novel objects in phobic (bag-avoiding) and non-phobic (bag-approaching) monkeys, the results of the previous study and the present one seem to diverge. In the previous study phobics and non-phobics only differed in their reactions to the bag, and not in their reactions to the novel objects used then: a rat. a cat, a big metal box and a big plastic doll (see Timmermans et al., 1986). In the present study phobics avoided two big novel objects, a triangle and a chair, but non-phobics approached these objects. Small novel objects, however, were approached by almost each *S* regardless its previous reaction to the big paper bag. The effect of size was demonstrated most clearly by the difference between reactions to the big -meanwhile familiar- bag and the small -novel- bag. The striking dichotomy in phobic monkeys in their reactions to big and to small novel objects probably was due to the great difference in volume between the two classes of objects; the volume of small objects amounted only 5% of the volume of big ones.

The finding that phobics are avoiders and non-phobics are approachers seems to concur fairly well with the opinion of Barnett and Cowan (Barnett & Cowan, 1976; Cowan, 1983) that in rats avoidance and approach as reactions to novelty are individual characteristics. Suomi (1986) seems to hold the same view when he reports that rhesus monkeys that reacted fearfully to (not specified) objects at an early age, reacted the same way to objects of the same class at a later age.

Yet it is not clear whether the phenomenon of avoidance in our monkeys is identical to neophobia in rats as described by Barnett. Barnett (1975) emphasized that neophobia has two important features: " First, it is temporary: although the effect can last for weeks, usually the avoidance is overcome in a few days or even hours.... Second, neophobia is always observed when there is a change in an otherwise familiar situation" (Barnett, 1975, p. 48). Our monkeys did not overcome the avoidance of the paper bag. This might be due to procedural differences as Barnett introduced something novel and than left the situation unchanged while we presented the bag in 30 min sessions with

intervals of 24 h or more. In all, *Ss* used in the present study got, on an average, 50 half hour sessions spread over 8 blocks of tests in the course of 4 yr.

Contrary to what we expected to occur in view of the findings of the previous study (Timmermans et al., 1986) the avoidance reaction was not restricted to the bag. Meanwhile, the lack of difference in reactions to novel objects between phobics and non-phobics in the previous study can partly be explained. The rat and the cat were much smaller than the big novel objects used in the present study and the metal box was made of steel sheet which was well known to the monkeys as various parts of the cage were made of steel sheet. Recent observations showed that a construction made of steel sheet (of the size of the big object) built into the cage was not avoided. It remains puzzling why the plastic doll (Donald Duck), which was at least as big as the big paper bag and novel in several respects, was nevertheless approached. Years ago we noted a similarly puzzling reaction in two juvenile chimpanzees. The chimps approached the Donald Duck doll but they fled into the highest corner of the cage when a pumpkin was offered.

In an attempt to answer the question what causes a monkey to become an avoider various aspects must be considered. Röder et al. (1989) have shown that rearing condition is an important factor when the probability that a monkey becomes an avoider is at stake. That both types (phobics and non-phobics) occurred in the mother-reared group may be explained by differences in early experiences as a consequence of differences in maternal behaviour. But concerning the surrogate-reared group we draw attention to the fact that surrogate rearing not only is a mother deprivation technique but as much a technique to preclude differential rearing experiences. So differences among surrogate-reared monkeys could have been caused by genetical or pre- and perinatal factors. As for genetics factors, selective breeding of timid strains has been shown to be successful with rats, mice and dogs, moreover, early physiological responses to challenge, which predicts fearfulness at a later age, were found to be more similar among siblings than among unrelated rhesus monkeys (Marks, 1987).

Then there is the question of the development of persistent avoidance of big novel objects in our tests situation. According to Rachman (1977) any neutral stimulus that makes an impact at a time fear is evoked may become a fear provoking signal. During the tests our monkeys were submitted to, two fear evoking events occurred: the young monkey

was separated from its (surrogate) mother and cage mates, and, a big novel object was presented to it. Phobic as well as non-phobics *Ss*, however, approached small novel objects that were presented in the same setup as the big ones. This finding renders conditioning to aspects of the setup a less plausible explanation for the acquisition of the phobic reaction.

The question which of the numerous differences between a mother and a surrogate mother are affecting the probability of becoming or not becoming phobic is subject of current experiments in which mobility of the mother and the surrogate mother is the central variable.

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Chapter 3

Effects of reducing the mother's radius of action on the development of mother-infant relationships in long-tailed macaques

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Abstract. Long-tailed macaque, *Macaca fascicularis*, mothers, but not their infants, were limited in their radius of action to a small part of the harem-group cage. The behaviour of infants and the mother-infant relationship in these restrained dyads and in unrestrained dyads were compared during the first half year of life. Restraining the mother had no effect on the mother-infant relationship. Furthermore, there was only one effect on the infants' development, namely that infants of restrained mothers were on the average 11 weeks older when they went beyond arm's reach of their mothers. This retardation in development of these infants' radius of action can be explained by infants being unwilling to enter the unfamiliar environment which could not be explored with the mother nearby.

Introduction

The natural mother is generally considered to serve as a secure base from which an infant explores the environment and engages in social behaviour. For the infant the environment contains a multiplicity of novel stimuli which elicit exploratory behaviour but also induce arousal. If over-aroused, the infant seeks contact with its mother to which arousal reducing properties are attributed (Baldwin & Baldwin, 1977). As novel stimuli become familiar, and less arousing, the infant has less need for arousal reduction. Growing up without a natural mother has short-term as well as long-term effects on behaviour. In social behaviour these effects consist of problems in developing an affective bond with a conspecific (Harlow & Harlow, 1965). In exploratory behaviour the effects consist of avoiding novelty (e.g. Sackett, 1972) and large novel objects (Timmermans et al., 1986; Vochteloo et al., 1991).

A second role of the mother during the development of the infant is to stimulate her infant to become independent by rejecting it more and more and by increasing the distance between her and her infant (Hinde & Spencer-Booth, 1968).

The mother-infant relationship can be influenced by several factors such as the attributes of both partners and environmental circumstances. In rhesus monkeys, *Macaca mulatta*, multiparous mothers reject their infants more frequently (Seay, 1966) and are less protective towards daughters (Hooley & Simpson, 1981) than primiparous mothers. White & Hinde (1975), however, did not find substantial differences between primiparous and multiparous mothers. The rank of a mother within a group also effects her maternal behaviour. Subordinate mothers restrain their infants more and therefore these infants have more contact with their mothers than infants of dominant mothers (White & Hinde, 1975;

Altmann, 1978; Sackett et al., 1982).

Besides these factors, the mother-infant relation is influenced by the social setting. The presence of conspecifics during the first stage of the infant's development affects the behaviour of the mother towards her infant. During the first 3 months of life infants are more restrained by their mothers if the mother is housed in a group than when the mother is individually housed (Wolfheim et al., 1970; Castell & Wilson, 1971; Hinde, 1971; Kaplan, 1972). Individually housed mothers more often punish and reject their infants, while mothers in a group to a greater extent maintain proximity and make contact with their infant (Wolfheim et al., 1970; Castell & Wilson, 1971; Kaplan, 1972).

In these studies on social variables both the mother and the infant were isolated and both subjects were enclosed in a small cage (Wolfheim et al., 1970; Castell & Wilson, 1971; Kaplan, 1972). The differences in the mother-infant relationship, found between group housed and individually housed mother-infant dyads, could therefore have been caused by social factors, by factors related to restraining the subjects, or by both. The non-social environment may also have influenced the mother-infant relationship. In Jensen et al.'s (1968) study, in an impoverished environment the physical contact between infant and mother was intensified and the development of the infant was retarded.

To determine the role of the mother in maintaining proximity, one should manipulate the opportunity of the mother to change the distance between herself and her infant without affecting the infant's ability to change the mutual distance. By not restraining the infant it is also possible to determine if an infant is willing to go beyond arm's reach of the mother into the environment in which it has not been before with its mother nearby. Restraining the mother in her radius of action, however, should not alter her familiar social and non-social environment. In this way, one could determine how the role of the mother in maintaining proximity affects the development of independence in her infant.

In this study female long-tailed macaques, *Macaca fascicularis*, were restrained in their radius of action by placing them in a small part of the familiar cage which they shared with the group they belonged to. Their infants were allowed to leave the separation cage and enter the cage of the group. Mothers and infants of the control group were allowed to move freely through the whole cage.

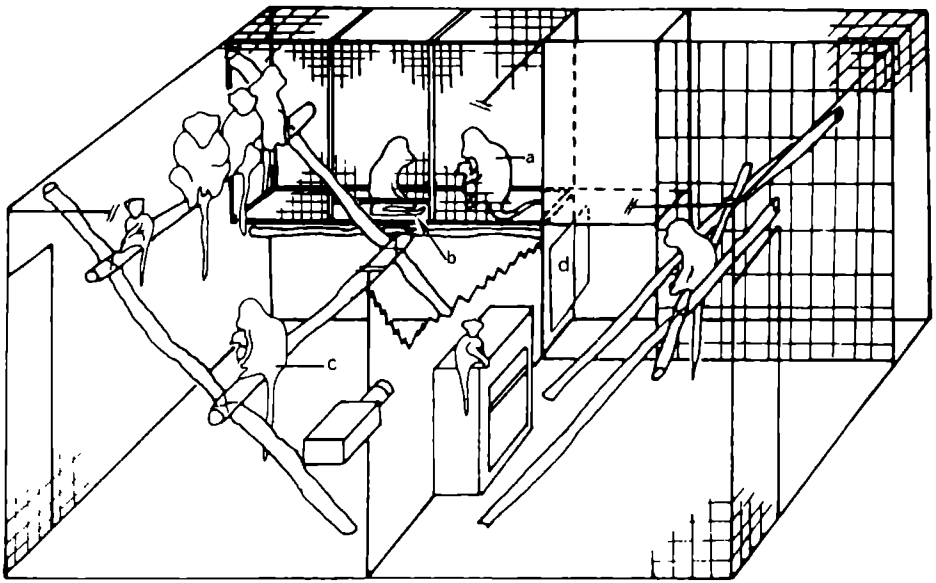

Fig. 1. *Experimental Set-up. Restrained mother (IMR-group) (a), slit in the netting (b), unrestrained mother (MMR-group) (c) and open passage between both compartments (d).*

Methods

Subjects and Housing

Long-tailed macaques born in harems in the laboratory, were used as subjects. Eighteen infants, with their mothers, were observed from 4 to 26 weeks. The subjects lived in one of three harem groups. Each harem group consisted of one adult male, four to nine adult females and a number of young varying between 0 and 3 years of age. The harem groups were housed in identical cages in separate rooms (see Fig. 1). The wire-netting cages measured 4.0 x 3.8 x 2.0 m. Each cage was divided into two compartments by an opaque partition. This partition was fitted with a sliding door which could be closed. Both compartments were provided with horizontal and vertical poles. A number of small pieces of wood and plastic bottles served as toys. Against the rear side of the left

compartment of each cage, at the height of 1 m, a small wire-netting cage was constructed, measuring 1.9 x 1.0 x 1.0 m (see Fig. 1). This separation cage was divided into three equal parts (.65 x 1.0 x 1.0 m) by two netting sliding doors. Each part was provided with a horizontal wooden shelf and a toy. In the front side of each part of the separation cage there was a slit through which a young monkey (but not an adult one) could pass. The mesh of the wire-netting of the separation cage permitted limited physical contact between the occupants and the other monkeys.

The floor of the cage of the harem was covered with wood chips which were changed bimonthly. The monkeys were fed twice a day with Monkey Chow (Hope farms). Water was provided ad libitum through some nipples. The lights were on from 08.00 to 20.00 hours.

Procedures

Subjects born between January 1988 and August 1990 were assigned to one of two groups. The experimental group consisted of young monkeys whose mothers were restrained in their radius of action by housing them in the separation cages: Immobile Mother Reared (IMR). The control group consisted of young monkeys whose mothers were not restrained in their movements: Mobile Mother Reared (MMR). To prevent disturbance of the social structure of a harem group, we decided that in each harem group only two females should occupy the separation cages at the same time. If two infants were born in the same harem group within 30 days, one infant was assigned to the IMR group and the other to the MMR group, in observance of the former rule. This way of assigning subjects to groups, did not allow us to consider the infants' gender, though we were aware of reported differences in maternal treatment of male and female infants (Mitchell, 1968; Simpson, 1983; Eaton et al., 1985; Johnson & Southwick, 1987). Infants of mothers that gave birth a second time in the course of the investigation were assigned according to the criteria mentioned above, irrespective of the assignment of the first infant. Both groups consisted of nine subjects. The IMR group included six male and three female infants. The MMR group included seven females and two males.

A subject that was assigned to the experimental group (IMR) was put into a separation cage with its mother within 2 days of birth. In addition, to prevent any

disturbed behaviour in the female, the sliding door between two parts of the separation cage was removed and the mother was given a female companion of her own harem group. Thus during the whole observation period two adult females with one or two infants lived in two interconnected parts of the separation cage. The companion female had an infant for an average of 50% of the observation period. The third part of the separation cage was not used. During the observation period of a subject, the harem group always included one or more other young monkeys.

Observations were made twice a week from the fourth week until the 21st week, and once a week from the 21st week until the 26th week of birth. The behaviour of the infant and of the mother towards her infant was recorded continuously during sessions of 45 min by means of a remote control video camera. Frequency and duration of specific behaviour patterns were registered on an event recorder (MORE Observational Systems). The start of a session was randomly scheduled across the week between 09.00 and 17.00 hours.

Parameters

The parameters used here were partly adopted from Simpson et al. (1986). The following behavioural categories of infant and mother were calculated.

(1) Near mother: percentage of the observation time the infant spent within arm's reach of the mother (≤ 70 cm) without physical contact with the mother (except for brief touches).

(2) Away mother: percentage of the observation time the infant spent beyond arm's reach (> 70 cm) of the mother (MMR group) or was outside the separation cage (IMR group).

(3) Off mother: percentage of the observation time the infant was separated from the mother (1 plus 2). During Off mother the following behaviour patterns of the infant were scored: Social activity: manipulating of and playing with conspecifics (with the exception of the mother); Auto-activity: manipulating parts of the infant's own body (e.g. digit sucking and autogrooming); Exploration: manipulating objects or parts of the cage; Other: other behaviour (e.g. locomotion, eating).

(4) Infant makes: the number of physical contacts with the mother initiated by the infant

that lasted for more than 5 s and resulted in Contact (6).

(5) Mother makes: the number of physical contacts with the infant initiated by the mother that lasted for more than 5 s and resulted in Contact (6).

(6) Contact: percentage of the observation time the infant had physical contact with the mother in ventro-ventral position or was sitting on her lap; the infant did or did not have contact with a nipple.

(7) Infant breaks: the number of physical contacts (6) that were broken by the infant.

(8) Mother breaks: the number of physical contacts (6) that were broken by the mother.

(9) Mother avoids: the number of times the mother withdrew within 5 s of the infant approaching her to less than 30 cm, expressed as: absolute frequency, that is the number of Mother avoids per 1000 s observation time, and expressed as: relative frequency, that is the number of Mother avoids as a proportion of the number of Infant makes (4).

(10) Mother rejects: the number of times the mother prevented the infant making Contact (6) within 5 s of Infant makes (4), expressed as: absolute frequency, that is the number of Mother rejects per 1000 s observation time, and expressed as: relative frequency, that is the number of Mother rejects as a proportion of the number of Infant makes (4).

(11) Mother restricts: the total of the number of times the mother: (i) held her infant tightly as it tried to break (7), (ii) pulled back her infant that had already broken contact; and (iii) contacted her infant (5), expressed as: absolute frequency, that is the number of Mother restricts per 1000 s observation time, and expressed as: relative frequency, that is the number of Mother restricts as a proportion of the number of Infant breaks (7).

(12) Social contacts mother-infant: the number of brief touches exchanged between mother and infant that did not result in Contact (6).

(13) Contact other adult: percentage of the observation time the infant had ventro-ventral-contact with other adult monkeys.

Statistics

The observation period was divided into blocks of 2 weeks. The means per block

were polynomially transformed and consecutively analysed using a MANOVA trend analysis procedure and performed with SPSS (Norusis, 1990). Because the sex ratio of the two groups was unbalanced two factors and their interaction were analysed (group, sex and group x sex). Only group data are presented. Where sex or sex x group differences are found, they are mentioned in the Results. In the relevant analyses the general difference in the mean is shown as F_{med}, the linear trend effects as F_{lin} (an upward/downward trend in % duration or frequency of a behavioural element), and the quadratic effect as F_{qua} (an accelerated or decelerated upward/downward development). In the figures a second order polynomial curve is fitted (Feldman et al., 1986).

Because of the possibility that differences between the two groups would only occur in a short period of time, the observation period was divided into five stages; stage 1 = weeks 5 - 8; stage 2 = weeks 9 - 12; stage 3 = weeks 13 - 16; stage 4 = weeks 17 - 20; and stage 5 = weeks 21 - 26. In every stage all parameters of the two groups were compared by a Mann-Whitney *U* Test. Over the whole period as well as per stage correlations (Pearson) were computed between the parameters. Further correlations (Pearson) per parameter between the five stages were computed.

One mother of the MMR group died when her infant was 5 months old. After her death only the behaviour performed while Off mother of this infant was used in the analysis.

RESULTS

Off mother

IMR and MMR subjects did not differ in the overall percentage of time Off mother ($F_{med(1,14)}=1.8$; Fig. 2a). In stage 5 (weeks 21-26, see Statistics) the IMR subjects were less Off mother than the MMR subjects ($U=17$, $p < 0.05$). In both groups the time the subjects were Off mother increased ($F_{lin(1,14)}=81.6$, $p < 0.001$). The time the subjects were Off mother in stage 3 was positively correlated with the time Off mother in stage 4 and 5 (stage 3 - stage 4 $r_p =0.667$, stage 3 - stage 5 $r_p =0.74$, stage 4 - stage 5 $r_p =0.736$, $p < 0.01$).

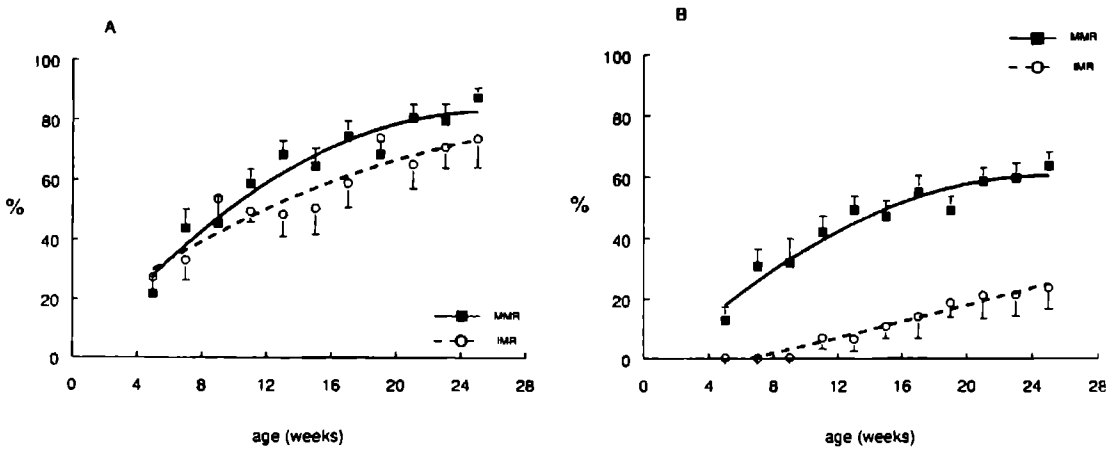

Fig. 2. *Mean percentage of the observation time (± SEM) per 14-days period that infants were (A) Off mother and (B) Away mother. The line represents the second order polynomial curve.* O *: Restrained mother group (IMR);* ■ *: Unrestrained mother group (MMR).*

Away mother

During the whole period and in every stage the MMR group spent more time Away mother than the IMR group ($F_{med(1,14)}$=52.6, $p < 0.001$; Mann-Whitney U test, $p < 0.001$; Fig. 2b). The average age at which a IMR subject left the separation cage for the first time was 16 weeks (range= 9 - 31 weeks). The increase in Away mother in the course of the observation period was significant ($F_{lin(1,14)}$=35.2, $p < 0.001$).

Exploration

The time spent on exploratory behaviour did not differ between both groups ($F_{med(1,14)}$= 0.11; Fig. 3a). The increase of exploratory behaviour in the course of time was significant ($F_{lin(1,14)}$=19.5, $p < 0.001$). Further, it appeared that time spent on exploration correlated positively with time Off mother (Off mother - Exploration: stage 2 r_p =0.704, $p < 0.01$; stage 3 r_p =0.834, $p < 0.001$; stage 4 r_p =0.659, $p < 0.01$).

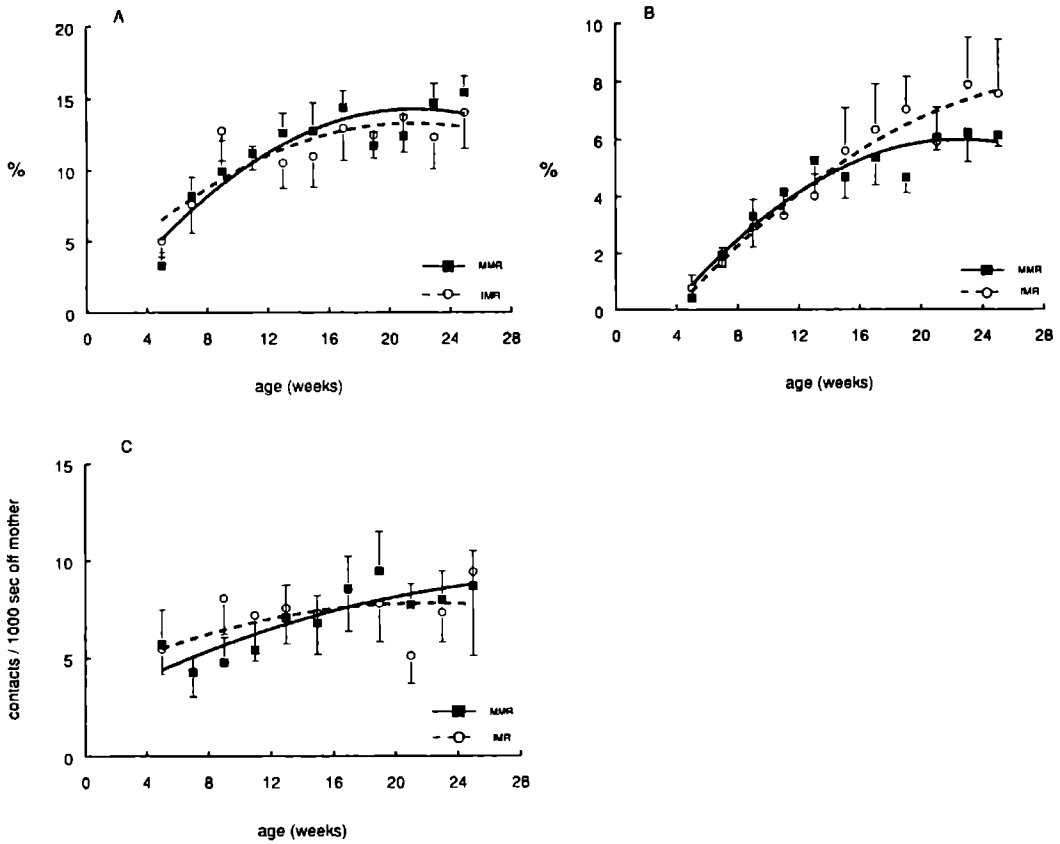

Fig. 3. *Mean percentage of the observation time (± SEM) per 14-days period that infants spent on (A) Exploration and (B) Social activity. (C) The mean frequency (± SEM) of Social contacts mother-infant, when the infants were Off mother. The line represents the second order polynomial curve.* O *: Restrained mother group (IMR);* ■ *: Unrestrained mother group (MMR).*

Social activity

Despite the fact that IMR subjects had a smaller radius of action than MMR subjects, they did not differ from MMR subjects in the time spent on social interactions

with conspecifics apart from their mother ($F_{med(1,14)}$=0.0; Fig. 3b). The accessibility of the separation cage to other subjects (during the whole observation period) and the presence of another infant of a companion restrained mother (50% of the observation period) gave sufficient occasion for social interactions. The time spent on Social activity increased during the observation period ($F_{lin(1,14)}$=37.0, $p < 0.001$).

Notwithstanding the fact that IMR subjects spent more time within arm's reach of their mothers, they did not have more Social contact mother-infant than MMR subjects ($F_{med(1,13)}$=0.0; Fig. 3c). During the whole period there was a group x sex interaction. Male IMR subjects had more and female IMR subjects had less Social contact mother-infant compared to their sex-mates of the MMR group ($F_{med(1,13)}$=4.72, $p < 0.05$).

All subjects were low in Contact other adult, and the groups did not differ in this behaviour. Out of nine IMR subjects, two in stage 1, one in stage 2, two in stage 3, three in stage 4, and four in stage 5 had some Contact other adult (average percentage of time during the whole observation period = 0.53%, range 0.5 - 4.6%). Three subjects did not have any Contact other adult. The subjects of the MMR group showed a similar distribution in Contact other adult (average percentage =0.97%, range 0.4 - 11.8%). Also in this group three subjects did not have any Contact other adult.

Mother-Infant relationship

Mother and infant makes and breaks

Restraining the radius of action of the mother did not affect Mother makes and Infant makes nor did it affect Mother breaks and Infant breaks (Infant makes: $F_{med(1,13)}$= 1.28; Infant breaks: $F_{med(1,13)}$=0.03; Mother makes: $F_{med(1,13)}$=0.85; Mother breaks: $F_{med(1,13)}$=1.51). During the whole observation period the number of contacts that were made and broken by mothers as well as by infants decreased. The frequency of Mother makes decreased from 5.2 per h in stage 1 to 0.75 per h in stage 5 ($F_{lin(1,13)}$=12.2, $p <$ 0.01), whereas the frequency of Infant makes declined only from 6.9 and 8.6 per h in respectively, stage 1 and 2 to 4.3 per h in stage 5 ($F_{lin(1,13)}$=11.5, $p < 0.01$). The infants' part in making contacts increased from 60% in stage 1 to 85% in stage 5 (Fig. 4a). In the same period Mother breaks decreased from 2.4 to 1.1 per h ($F_{lin(1,13}$=3.89, ns), and, Infant breaks from 9.95 to 4.3 per h ($F_{lin(1,13)}$=9.6. $p < 0.01$). During the whole observation

period the mothers' as well as the infants' part in breaking contact stayed the same (ratio 1:4; Fig. 4b).

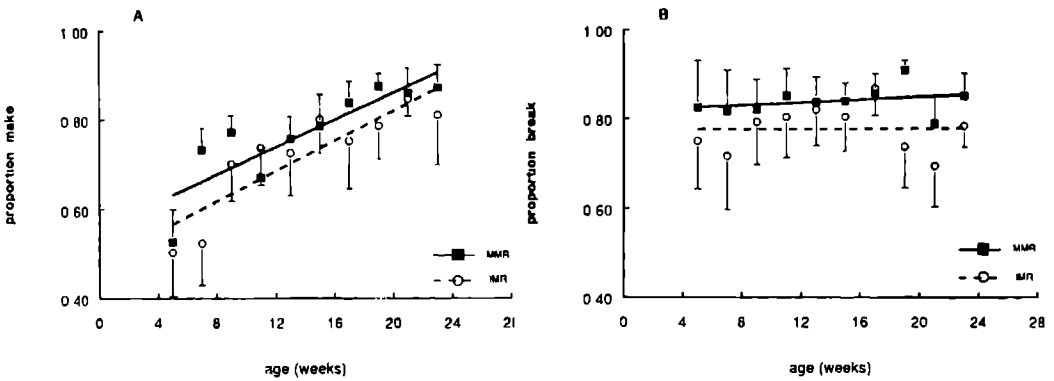

Fig. 4. *Infant's part (mean ± SEM) in (A) making and (B) breaking contact, presented as a proportion of total contacts made and total breaks, respectively. The line represents the linear trend.* O *: Restrained mother group (IMR);* ■ *: Unrestrained mother group (MMR).*

Rejecting, avoiding and restricting behaviour of the mother

In no stage of the observation period was there any difference between the groups in maternal behaviour, either in absolute, or in relative, frequency.

Restraining mothers in their radius of action did not affect their rejecting and avoiding infants. The absolute frequency of Mother rejects as well as the absolute frequency of Mother avoids increased till the infants were 17 weeks old and after that decreased until the end of the observation period (week 26; Fig. 5a,b) (Mother rejects: $F_{qua(1,13)}=10.5$, $p < 0.01$; Mother avoids: $F_{qua(1,13)}=70.0$, $p < 0.05$). In addition, the relative frequency of Mother rejects and the relative frequency of Mother avoids did not differ between groups. The relative frequency of Mother rejects increased ($F_{lin(1,13)}=8.14$, $p < 0.05$). It appeared that until the infants were 18 weeks old Mother rejects increased and remained constant after this age (Fig. 6a). The relative frequency of Mother avoids was approximately constant during the whole observation period (Fig. 6b).

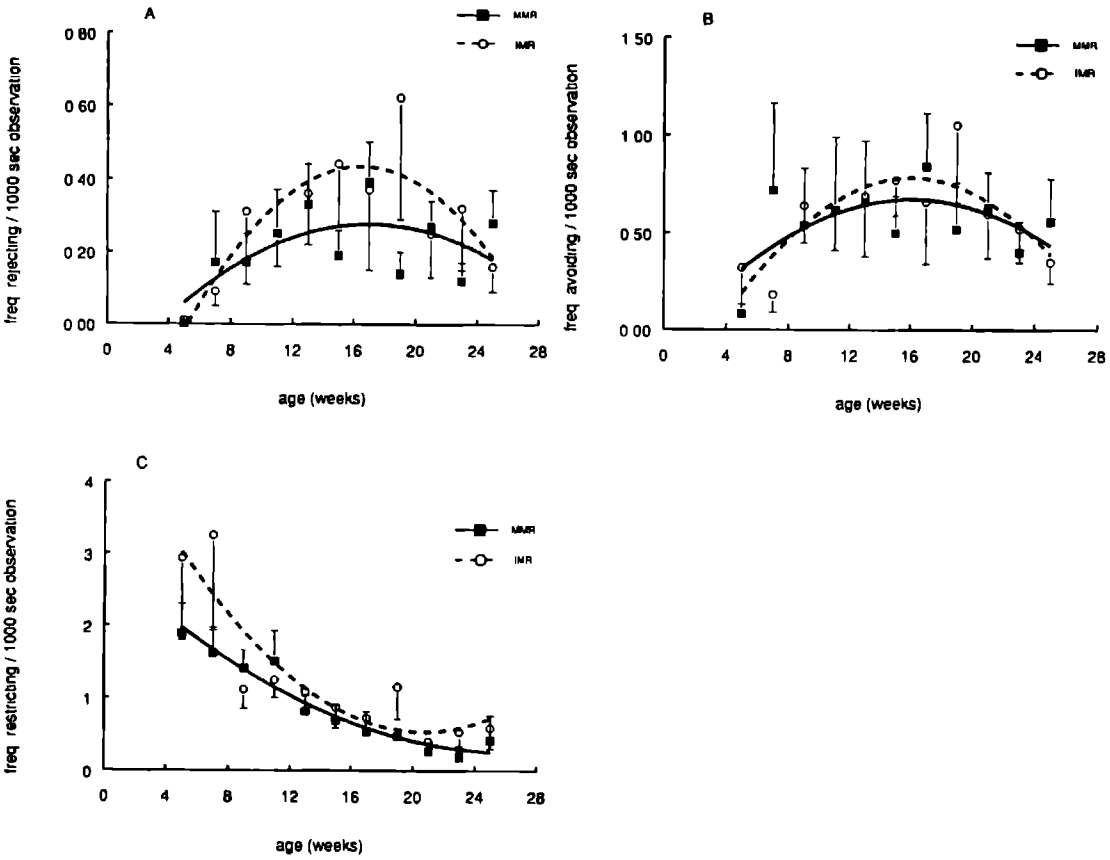

Fig. 5. *The mean frequency per 1000 s observation time (± SEM) of (A) Mother rejects, (B) Mother avoids and (C) Mother restricts. The line represents the second order polynomial curve.* O *: Restrained mother group (IMR);* ■ *: Unrestrained mother group (MMR).*

The restricting behaviour of the mothers was not affected by radius of action. The parameter absolute frequency of Mother restricts fell from 2.5 (stage 1) to 0.2 (stage 5) per 1000 s observation time ($F_{\ln(1,13)}=8.89$, $p < 0.05$; Fig. 5c). Male IMR subjects (N=6) were more restricted by their mother than the other subjects (group x sex interaction:

$F_{med(1,13)}=5.8$, $p < 0.05$). The relative frequency of Mother restricts showed a slight decline during the whole observation period ($F_{lin(1,13)}=4.52$, $p = 0.053$; Fig. 6c).

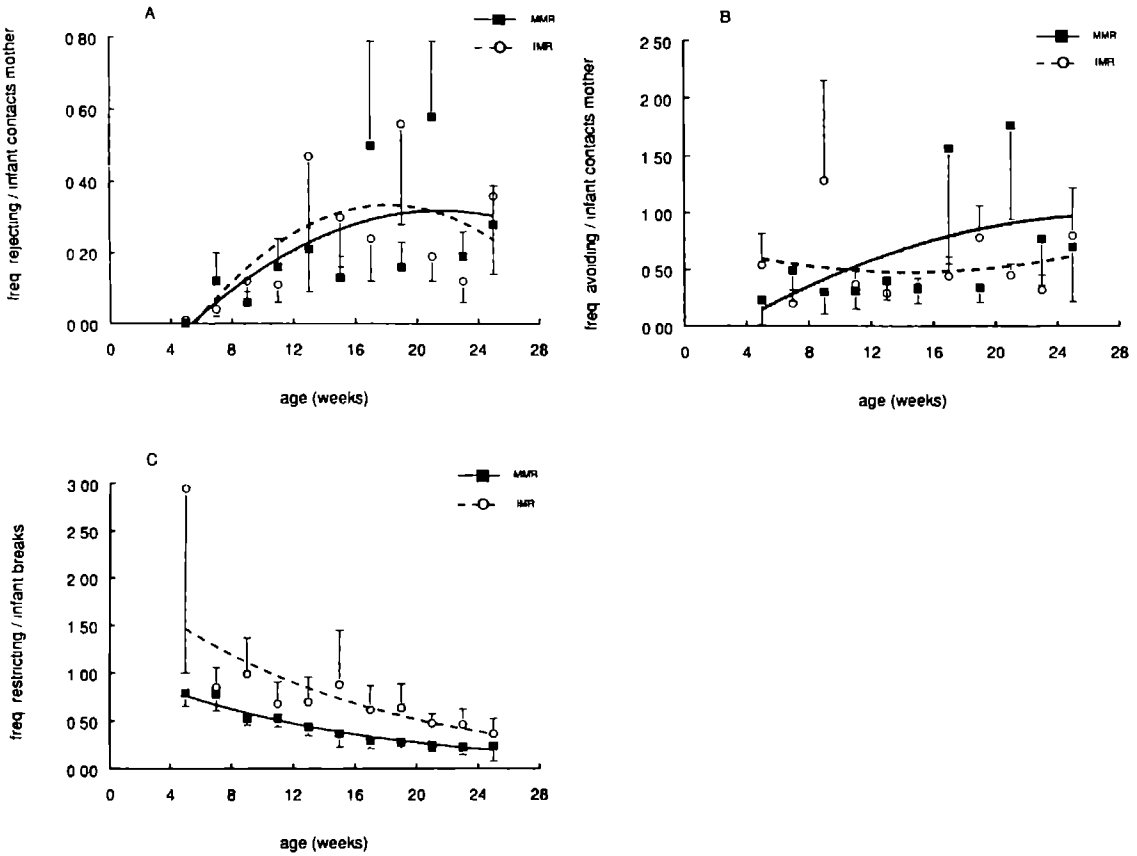

Fig. 6. *The mean frequency (± SEM) of (A) Mother rejects and (B) Mother avoids presented as proportion of the contacts made by the infant, and the mean frequency (± SEM) of (C) Mother restricts as a proportion of the contacts broken by the infant. The line represents the second order polynomial curve.* O *: Restrained mother group (IMR);* ■ *: Unrestrained mother group (MMR).*

Discussion

Restraining mothers in their radius of action did not have any effect on their maternal behaviour; the only effect it had on the infant was that infants of restrained mothers went beyond arm's reach of their mothers (Away mother) at a later age than infants of mothers that were not restrained in their radius of action.

Hinde & Spencer-Booth (1968) and Berman (1980) reported that in rhesus monkeys the mother is predominant in maintaining proximity during the first months after birth of an infant. In our experimental set-up, however, the mothers that were limited to the separation cage, were not capable of maintaining proximity (retrieving or following) when the infant had left the separation cage. Only the infants of these mothers were able to determine the distance between themselves and their mother in the separation cage. These infants, however, rarely went beyond arm's reach (left the separation cage) during the first months. They went away at a later age and spent less time beyond arm's reach of the mother than the infants of the control group. It appeared that infants of restrained mothers stayed close to their mothers although the mothers could not take part in determining the distance. Further, mothers that stayed in the separation cage were not able to manipulate the distance by leaving their infant. Its seems unlikely that the unrestrained mothers influenced the distance in the first 2 months by enlarging the distance. In the rhesus monkey in this phase of development the mother is mainly responsible for maintaining proximity (Hinde & Spencer-Booth, 1968; Berman, 1980; see also Altmann, 1978).

In rhesus monkeys the part of the mother in maintaining proximity decreases 3 - 5 months after birth of the infant (Hinde & Spencer-Booth, 1968; Berman, 1980). This decrease in maternal efforts to maintain proximity is important for the development of independence of the infant (Berman, 1980; Hinde, 1983). At the age of 3 - 6 months the infants of our restrained mothers increasingly took the initiative in going beyond arm's reach of their mothers, although the mothers could never induce such a distance between them and their infants. It appeared that infants (finally) went away from their mothers without being stimulated to do so by departures of the mother.

The most plausible explanation of the difference between infants of restrained and unrestrained mothers in going away seems to be that infants of restrained mothers were not familiar with the environment outside the separation cage. Infants of unrestrained mothers were carried around the whole cage and got to know the environment with their mothers nearby. According to Baldwin & Baldwin (1977) the availability of arousal reducing stimuli (such as the mother) can have a positive effect on the development of exploratory behaviour and play of the infant (see also Bronson, 1968). As hypothesized by Rosenblum (1971), a complex environment can force young infants to stay close to the mother rather than to explore. This may be why infants of restrained mothers did not enter the harem cage in the first three months.

The general progress in time that our infant monkeys did not have contact with their mother (Off mother) corresponds with the findings in rhesus monkeys (Hinde & Spencer-Booth, 1968; Berman, 1980; Simpson et al., 1986). In the first half year, our infants of restrained mothers were as much Off mother as infants of mothers that moved around freely. Castell & Wilson (1971) and Wolfheim et al. (1970) studied pigtail monkeys, *Macaca nemestrina*, and compared group-housed mother-infant dyads with individually housed mother-infant dyads that could see and hear other dyads but could not have physical contact with them. They found that in the first 3 months infants in individually housed dyads spent more time Off mother than infants in group-housed dyads. In rhesus monkeys a similar effect was found (Hinde, 1971; 1983). However, the condition in which individual rhesus and pigtail dyads were housed, differed from our condition in the separation cage. In our set-up all dyads were in the company of one other adult female (sometimes with an infant) and infants of the control group could also enter the separation cage. So it seems that individual housing of mother-infant dyads causes an increase in Off mother when contact with other conspecifics is impossible. Further Castell & Wilson (1971) found that in the fifth month infants of individually housed dyads were less Off mother than infants reared in a group. We found a similar difference in time Off mother between the infants of restrained mothers and infants of unrestrained mothers. One explanation for this difference can be found in the relatively impoverished environment infants of restrained mothers lived in, and that resulted in a closer bond between the mother and her infant as concluded by Jensen et al. (1968). Another explanation can be

found in the inability of restrained mothers to withdraw. Our unrestrained mothers were able to go out of sight of their infants (to the other cage compartment), and then their infants were less likely to seek contact with them.

Wolfheim et al. (1970), Castell & Wilson (1971) and Kaplan (1972) reported that individually housed mothers punished and avoided their infants more than group-housed mothers did. They explained these differences by referring to the size of the cage. A small cage, according to Kaplan (1972), leads to more dyadic interactions and thus the mother punishes and avoids her infant more often. Moreover, Rosenblum suggested that lack of social interactions with other monkeys enhanced the level of infant-mother contact, which might stimulate an early onset of the maternal abdyadic pattern (Rosenblum, 1971, p. 355). Although our IMR subjects spent a lot of time in the separation cage near their mothers, the number of contacts between mother and infant did not differ from the number of contacts in MMR subjects, and, probably as a result of this, maternal behaviours such as rejecting and avoiding did not differ either. It seems that the presence of other familiar monkeys and the availability of contact with other infant monkeys gave the infant as well as the mother enough opportunity for other social interactions.

We did not find a positive correlation between the time the infant had no contact with the mother (Off mother) and rejecting behaviour of the mother, as was found in rhesus monkeys (Hinde & Spencer-Booth, 1968; Berman, 1980). Neither did we find any relation between rejecting or restricting behaviour of the mother and the time the infant was Off or Away mother.

The most rejection and avoidance behaviour by mothers occurred between weeks 12 and 20, which is in agreement with findings in rhesus monkeys (Hansen, 1966). The gradual decrease of maternal restriction we found also corresponds with results obtained with other macaque species (Hinde & Spencer-Booth, 1968; Rosenblum, 1971, Simpson et al., 1986). Male infants are more restricted than females in Japanese macaques, *Macaca fuscata*, living in colonies (Eaton et al., 1985), in multiparous rhesus mothers (Hooley & Simpson, 1981), and in squirrel monkeys, *Saimiri sciureus* (Rosenblum, 1974). We also found that among IMR subjects males were more restricted than females.

The increase we found in the infants' part in making contact with their mothers corresponds to reports by Altmann (1978) on yellow baboons, *Papio cynocephalus*, and by

Berman (1980) and Simpson et al. (1986) on rhesus monkeys.

If the degree of independence of an infant is defined as usual in terms of the distance between mother and infant (Rijt-Plooy & Rijt, 1987) we conclude that restraining a mother in her radius of action delayed the development of independence of her infant. This retardation then is not a result of direct maternal behaviour but, most likely, a result of unfamiliarity of the infant with the environment which could not be explored with the mother nearby. In this view the behaviour of the mother, like leaving and rejecting her infant, is not a prerequisite for the development of infants' independence.

Acknowledgments

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Chapter 4

The Effects of Reducing the Mother's Range of Action on the Behavioural Development of Infant Long-Tailed Macaques

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Accepted: Primates

Abstract. In order to study the effects of the mothers' range of action on the development of their infants, mother long-tailed macaques were restrained in their range of action by confining them to a small part of a large cage The restrained mothers belonged to a harem group that lived in the same large cage In contrast with their mothers, infants could leave the cage in which their mothers were restrained The control group consisted of infants that grew up with unrestrained mothers in the same harem group The infants were compared in their behavioural development and in the development of their range of action during the first year of their life It appeared that infants of restrained mothers were initially retarded in the development of their range of action At the end of the first year infants of restrained mothers did not differ anymore from infants of unrestrained mothers It is concluded that the maternal range of action only temporarily affects the development of the infant's range of action

Introduction

During the development of a young non-human primate the distance between mother and young gradually increases. This increase in distance can be taken as an indication of a growing independence of the young (Rijt-Plooy & Plooy, 1987). The development of this independence can be affected by factors originating from the physical environment like varying foraging demands (Andrews & Rosenblum, 1991; see also Lee, 1986) and environmental enrichment (Jensen, Bobbitt & Gordon, 1968), but also by social factors. Especially during the first months of life a young spends more time in physical contact with its mother when the dyad is living in a group than in case the dyad is living separately (Hinde & Spencer-Booth, 1968; Wolfheim, Jensen & Bobbit, 1970; Castell & Wilson, 1971; Kaplan, 1972). On the other hand the availability of other conspecifics benefits the development of social play. That, together with exploration is seen as an important factor for adequate adult functioning (Dolhinow & Bishop, 1970; Welker, 1971; Poirier, Bellisari & Haines, 1978; McGrew, 1977; MacDonald, 1986).

Of special importance are the characteristics of the mother. Maternal behaviours like restriction and rejection affect the degree to which a young becomes independent of the mother (Hinde & Spencer-Booth, 1968; Altmann, 1980). These maternal behaviours also can influence the development of social skills of the young (Johnson, Gilbert & Herdt, 1979) and the willingness of the young to expose themselves to novelty (Fairbanks & McGuire, 1988).

Though it is well known that a monkey mother carries her young about in the environment the role of this behaviour in relation to the development of the young has not

been experimentally studied yet. Carried by the mother the young gets into contact with all kinds of environmental stimuli. According to several authors the proximity of an attachment figure reduces the young's fear of novelty (e.g. King, 1966; Bronson, 1968 a,b; Dolhinow & Bishop, 1970; Baldwin & Baldwin, 1977; Miller, Bard, Juno & Nadler, 1986). This enables the young to become more and more familiar with the environment resulting in an increase in the distance between the young and its mother (Baldwin & Baldwin, 1977). Next to other features of the mother, e.g. rank, maternal rejection or restriction, her range of action provides the young with experiences that may be of importance for its development of self-reliant exploration of the environment.

Rearing young monkeys under restricted conditions (Menzel, 1964; Sackett, 1972; Elias & Samonds, 1973) and on surrogate mothers (Sackett, 1972; Timmermans, Röder & Hunting, 1986; Röder, Timmermans & Vossen, 1989) induced behavioural disorders among which the avoidance of novelty. This behaviour is mostly attributed to a lack of maternal care. However, these rearing conditions do not only deprive young monkeys from maternal care but also withhold them from the opportunity to explore the distant environment in the vicinity of an attachment figure, since surrogate mothers generally are fixed.

To study the effects of the maternal range of action upon the development of their young, we restrained long-tailed macaque mothers by placing them in a separation compartment in the cage of the harem group they belonged to. Their young could leave this separation compartment and enter the harem cage. A control group consisted of young, the mothers of which could freely move around in the harem cage.

Previously we reported that during the first half year of their life infants of restrained mothers stayed in the proximity of their mothers whereas infants of unrestrained mothers did leave their mothers (Vochteloo, Timmermans, Duijghuisen & Vossen, 1993). As it was of interest to know whether this difference in development of radius of action, due to restraining the mother, was temporary, we continued to study the development of radius of action for another half year and, next to this, we studied the development of other behaviour.

Methods

Subjects and Housing.

Eighteen long-tailed macaques (*Macaca fascicularis*) born in the laboratory and reared by their mothers were used as subjects. The subjects and their mothers were members of harem groups. Each harem group, of which there were three, consisted of one adult male, four to nine adult females and a number of young between 0-3 years of age.

The harem groups were housed in three separate rooms in identical wire netting cages, measuring 4.0 x 3.8 x 2.0 m. (Fig. 1).

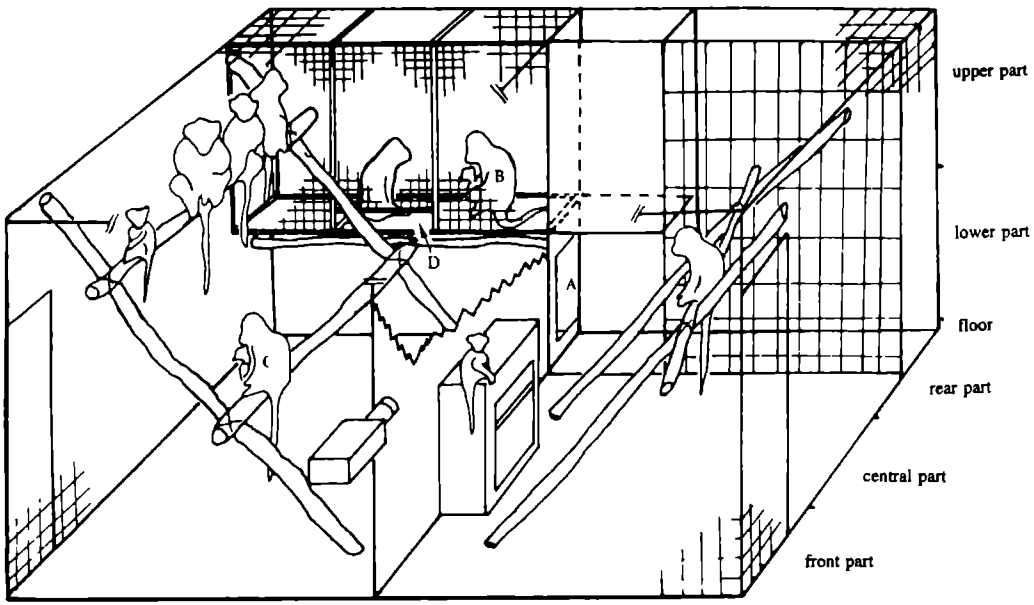

Fig. 1. *Experimental set-up for the MMR and IMR group. A. open passage between compartments, B. restrained mother (IMR-group), C. unrestrained mother (MMR-group), and, D. slit in the netting of the separation cage.*

A cage was divided into two compartments of equal size by an opaque partition. This partition was fitted with a sliding door which was usually open. Against the rear side of the left compartment of each cage, at the height of one meter, a wire-netting separation

compartment was constructed (1.3 x 1.0 x 1.0 m), which was used to confine mothers. This separation cage was provided with two horizontal wooden perches and a piece of wood or a plastic bottle as toy. In the front side of the separation cage there was a slit in the netting through which a young monkey (but not an adult one) could pass. The mesh of the wire-netting of the separation cage permitted limited physical contact between the occupants and the other monkeys of the harem.

The floor of the cages was covered with wood-chips which were refreshed bimonthly. Some pieces of wood and a few plastic bowls served as toys. The monkeys were fed twice a day with Monkey-Chow (Hope farms). Additionally, pieces of apple and cereals were given once a week. Water was provided ad libitum through nipples. The lights were on from 8.00 till 20.00 hours.

Rearing conditions

The subjects grew up in one of the following conditions:

- with their mothers that freely could move around in a harem cage (MMR = Mobile Mother Reared),
- with their mothers that were housed in separation cages within a harem cage (IMR = Immobile Mother Reared).

All subjects were born between January 1988 and August 1990. The MMR group consisted of 7 females and 2 males, and the IMR group of 3 females and 6 males.

MMR and IMR subjects lived in the same harems. In assigning the subjects to the IMR or MMR group we had to take into account that in each harem-group only two mothers could reside in the separation cages at the same time in order not to disturb the social structure of the harem-group. During the observation period we tried to have an equal number of subjects in both groups, in observance of the former rule. This way of assigning subjects to groups did not allow us to consider the infants' gender, although we were aware of reported differences in striving for independence (Berman, 1982; Welker & Witt, 1982; Eaton, Johnson, Glick & Worlein, 1985).

A subject of the IMR group was put into the separation cage with its mother within two days after birth. A mother of an IMR subject always had company of another adult female, which also could be a mother of an IMR subject. Thus during the whole

observation period the separation cage in a harem group always was occupied by two females and one, or (on the average during 50% of the total observation time), two subjects of the IMR group. The mother was released after one year.

Observations

Subjects were observed for half an hour once a week from 6 until 26 weeks of age and once a fortnight from 27 until 41 weeks of age. In the 50-th week the subjects were observed for one hour and a half. The observation periods were randomly scheduled across the week between 09.00 and 17.00 hours. During the observation period the activities of the animal were recorded by means of a remote control video camera. From the recordings the behaviour and location in the cage were continuously registered with an event recorder (More Observational Systems).

Parameters

In order to assess the behavioural development of the infant, during the period the mother was restrained, behaviour as well as range of action were registered.

Behaviours

Because the limited range of action of the mother may have effects on the time the infant was off mother, and on the development of exploration and social behaviour, these behaviours as well as autoactivity, attentivity, and locomotion and were scored. These behavioural parameters are presented in table 1.

Range of action

Because infants of restrained mothers could not get familiar with the environment in the presence of the mother, we were interested whether the limited range of action of the mother did affect the development of the range of action of her infant. In order to assess the range of action of a subject its location was recorded. For that purpose both cage compartments were divided into 9 locations by making 6 sections: 3 horizontal

Table 1. *Behavioural parameters recorded during the observations*

Behaviour	Definition
Off mother	the time the subject did not have contact with its mother (except for brief touches or tail-hanging)
Autoactive	grooming, sucking and manipulating own body parts
Attentive	looking in a certain direction accompanied by a tense posture
Locomotion	moving at least one body length
Exploration	manipulation of objects; a distinction was made between loose objects (e g wood chips, toys) and fixed objects (e g climbing poles, wire)
Social behaviour	physical interaction with a conspecific (e g play, tail-hanging, grooming)
Social mother	social behaviour directed at the mother (e g brief touches, tail-hanging, grooming)
Other	behaviours not defined above

sections (an upper and lower part, and the floor) and, 3 vertical sections (a front, central and rear part) (see Fig. 1). The range of action of a subject was assessed by means of two parameters: distance of the subject from the mother, and, utilization of space (time spent in several parts of the cage). Due to the increasing speed and mobility of the subject the distance between mother and subject could no longer be reliably measured after the 22-nd week.

The parameter "utilization of space" was necessary to compare the IMR with the MMR group concerning the time they spent in several parts of the cage while off mother. This parameter was used to assess at what pace subjects mastered to visit various parts of the cage. The utilization of space was expressed as the number of zones of the cage utilized. To obtain this measure we chose to distinguish six zones which coincided with the vertical sections of both cage compartments. The criterion for the utilization of a zone was that a subject spent at least 1 % of its time "off mother" in that zone.

Statistics

In order to compare behaviours and parameters for range of action of the MMR and IMR group, the data were divided into age-blocks of 28 days and expressed in

percentages of time "off mother". The means of the age-blocks were polynomially transformed and consecutively analysed using a MANOVA trend analysis procedure with rearing condition and gender as between group factors. Further a Mann-Whitney *U* test was used to analyse differences between groups in behaviours and range of action per age-block. In the figures presented a second order polynomial curve was fitted (Feldman, Hofmann, Gagnon & Simpson, 1986).

Changes in the number of zones utilized were analysed by a Friedman Two-way analysis of variance.

To analyse the differences between both groups in the distance of the subject from the mother the mean percentage of time "off mother" that a subject stayed at a certain distance from its mother was calculated. Between the MMR and IMR group the following comparisons were made:

-within arm's reach of the mother (< 0.7 m) in MMR subjects versus inside the separation cage in IMR subjects,

-0.7 - 2.0 m from the mother in MMR subjects versus outside the separation cage to 1.5 m from the separation cage in IMR subjects,

-more than 2 m from the mother in MMR subjects versus more than 1.5 m from the separation cage in IMR subjects.

Results

Effects of gender

There were no main effects of sex on the development of behaviours and range of action. Per age block the analyses revealed a few sex differences.

Between 28 - 32 weeks males spent less time "off mother" than females ($F_{med(1,14)}$= 10.3, p< 0.01). In the same age block males spent less time on "social mother" than females ($F_{med(1,14)}$= 10.0, p< 0.01). Between 32 - 36 weeks males spent less time in the upper part of the cage and more time on the floor than females (respectively: $F_{med(1,14)}$= 5.99, p< 0.05; $F_{med(1,14)}$= 5.61, p< 0.05).

Effects of rearing condition

Behaviours

Off mother The IMR group and the MMR group did not differ in percentage of time off mother ($F_{med(1,14)}$=2.19. Both groups showed an increase in percentage of time off mother ($F_{lin(1,14)}$=32.3, p< 0.01; Fig. 2).

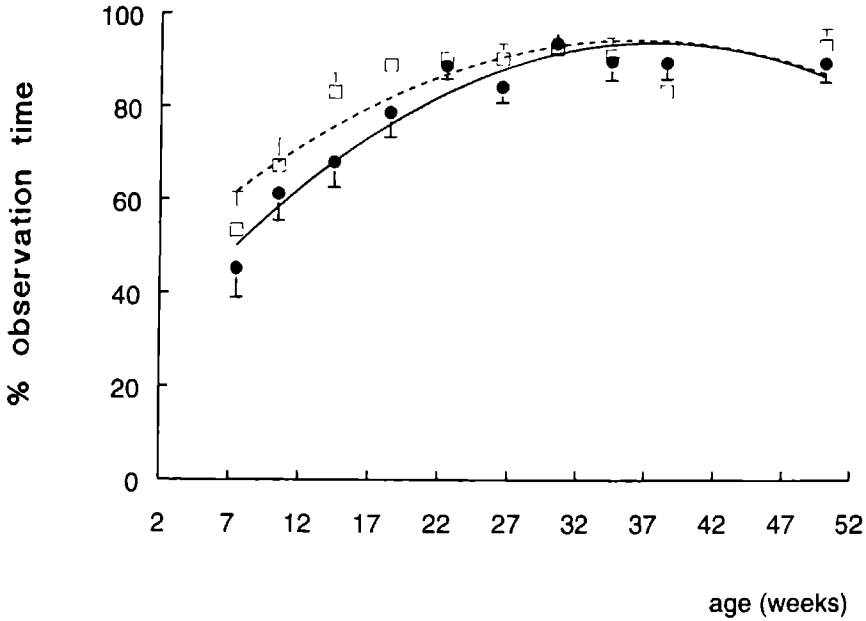

Fig. 2. *Mean percentage of observation time (± SEM) (per period of 28 days and second order polynomials) that infants of MMR and IMR group were off mother.*
● *:Restrained mother group (IMR);* □ *: Unrestrained mother group (MMR).*

Social behaviour During the whole observation period both groups spent about the same percentage of time on social behaviour ($F_{med(1,14)}$=1.09). Despite the fact that the subjects of the IMR group stayed more within arm's reach of their mothers (see below), they spent a lower percentage of time on "social mother" than the MMR subjects did ($F_{med(1,14)}$= 6.9, p< 0.05).

Exploration The groups did not differ in the percentage of time spent on exploration. However, the IMR group spent less time on exploration of loose objects than

the MMR group ($F_{med(1,14)}$= 5.15, p< 0.05). This difference in exploration of loose objects mainly occurred before the age of 20 weeks ($U \leq$ 18, p< 0.05). Between 9 and 16 weeks the IMR group explored more fixed objects than the MMR group ($U \leq$ 16, p< 0.05). In both groups exploration of loose objects increased ($F_{lin(1,14)}$=24.8, p< 0.01) whereas exploration of fixed objects decreased. In the IMR group this decrease of exploration of fixed objects was faster than in the MMR group ($F_{lin(1,14)}$=5.9, p< 0.05). The total percentage of time spent on exploration remained constant during the whole observation period.

Other behaviours The groups did not differ in percentages of time spent on locomotion, attentive and autoactive behaviour. In both groups the percentage of time spent on locomotion decreased ($F_{lin(1,14)}$=10.3, p< 0.01).

Range of action

Distance of the subject from the mother During the period that this parameter was scored (6 - 22 weeks) the subjects of the MMR group went farther away from their mothers than the IMR subjects did. The subjects of the IMR group remained most of the

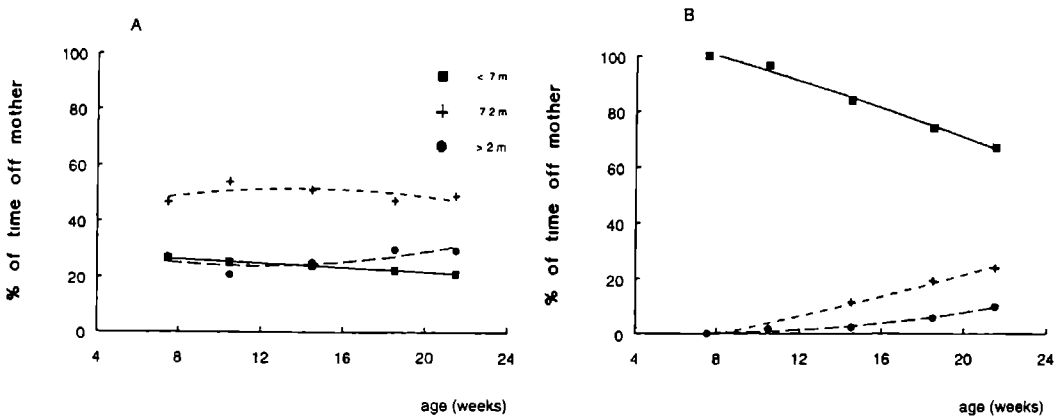

Fig. 3. *Mean percentage of the time off mother (per period of 28 days and second order polynomials) that infants of (A) the MMR group and (B) the IMR group stayed at distances of less than 0.7 m (■), between 0.7-2.0 m (+), and more than 2 m (●) from their mothers.*

time within arm's reach of their mothers, while the MMR subjects spent a lot of time outside arm's reach of their mothers. During this period as well as in each age-block of this period, the differences between the IMR and the MMR group were significant for each distance measured (< 0.7 m, 0.7-2.0 m and > 2.0 m) ($F_{med(1,14)} > 118$; $U \leq 6$, $p < 0.01$) (Fig. 3).

Utilization of space In order to compare the development of the range of action of the MMR and IMR group we used the criterion that a subject utilized a zone when it spent more than one percentage of its time "off mother" in that zone. It appeared that from 32 weeks on the IMR subjects utilized as many zones as the MMR subjects. Till the age of 32 weeks the IMR group utilized less zones (mean per subject = 3.3) than the MMR group (mean per subject = 5.6) did ($U \leq 15$, $p < 0.05$; Fig. 4). In the IMR group there was an increase in the number of zones utilized (Friedman $X^2=45.2$, $p < 0.01$).

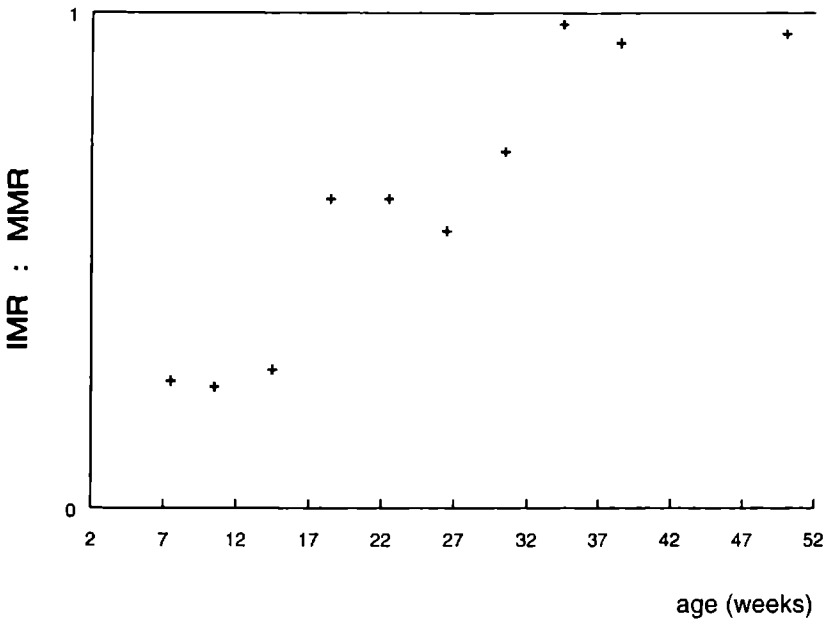

Fig. 4. *The ratios restrained mother group (IMR) : unrestrained mother group (MMR) for the number of zones utilized (per period of 28 days). A zone was scored to have been utilized if a subject stayed in it longer than 1% of its time off mother.*

Discussion

The most striking difference between young monkeys reared by restrained mothers (IMR) and young monkeys reared by unrestrained mothers (MMR) was that IMR young showed a temporary retardation in the development of their distance from the mother and of their utilization of the living cage.

In baboons, *Papio cynocephalus*, (Altmann, 1980) and in rhesus monkeys, *Macaca mulatta*, (Hinde & Spencer-Booth, 1968; Hinde, 1983) it was found that the time the infant spent beyond arm's reach of the mother was affected by maternal behaviour like rejection and restriction. We already reported that the rejective and restrictive behaviours of restrained and unrestrained mothers did not differ (Vochteloo et al., 1993). So the difference in distance from mother between the IMR and MMR group could not be due to differences in these aspects of maternal behaviour.

Also a difference in time off mother did not occur (Fig. 2). Thus staying on mother for a longer period cannot have caused the retardation in the development of the range of action. The causes of the retardation have to be looked for elsewhere.

Further, it appeared that the front wall of the separation cage (with a slit in the netting) did not act as a kind of barrier because we often saw that infants of unrestrained mothers already went in and out the separation cage at an age of 6 weeks. Notwithstanding this demonstration by peers the IMR subjects did not leave the separation cage till the age of 16 weeks on the average.

One might argue that the development of the range of action was retarded because restraining the mother affected the behaviour of group members towards the mother and her infant. However, if this had been the case a difference between restrained and unrestrained mothers in maternal behaviour as well as a difference between their infants in the time they had contact with their mothers was to be expected. As we did not find any difference in maternal behaviour between restrained and unrestrained mothers nor in the time infants of both groups had contact with their mothers (Vochteloo et al., 1993; see also Fig. 2), there are no reasons to assume that the behaviour of group members towards the restrained mother and her infant played a part.

Another item is that the difference in the development of the range of action between IMR and MMR subjects could be affected by the difference in sex-ratios. However, we found no sex effects. Further, in studies of Berman (1982), Welker & Witt (1982), and Eaton et al. (1985) it appeared that infant females stayed closer to their mothers than male ones. As the IMR group consisted mostly of males, the retardation of the IMR group can not be explained as an artefact of the difference in sex-ratio between the groups.

Our explanation of the retardation is as follows. In contrast with the unrestrained mothers, restrained mothers could not carry their infants through the cage. It is commonly accepted that a mother that carries her infant about is bringing the infant into contact with numerous stimuli and in this way gives the infant the opportunity to explore and to get acquainted with the environment while she is nearby and serves as a secure base (King, 1966; Bronson, 1968 a,b; Simonds, 1974; Baldwin & Baldwin, 1977; Bowlby, 1977; Miller et al., 1986). Lack of this opportunity seems to retard the development of the range of action of the young. The cause of this retardation could be that without maternal support, as it was the case in IMR subjects, the space outside the separation cage remained unfamiliar, which at first withheld the IMR subjects entering it. Going beyond arm's reach of the mother (out of the separation cage) coincided with entering a space that had not been visited in company of the mother. Probably for the same reason the subjects of the IMR group attained a maximal range of action at a much older age than the subjects of the MMR group. After 10 weeks MMR subjects showed no increase anymore in the distance from their mothers. Also the subjects of the MMR group then utilized most zones, whereas the IMR subjects no sooner were utilizing most zones than after 32 weeks.

A comparable difference in range of action as between the MMR and IMR group was found by Duijghuisen, Timmermans, Vochteloo and Vossen (1992) between long-tailed macaques reared with mobile or static surrogates. Young that from birth on regularly were moved through the cage on mobile surrogates went farther away from their surrogates than young that grew up with static surrogates only. As a consequence the young reared with mobile surrogates utilized a greater part of the cage.

Then there is the effect of the social context on the infant. In our experiment the social context consisted of group members of various ages. Rosenblum (1971)

hypothesized that for a young infant a complex environment at first is aversive, and the infant therefore needs the proximity of the mother. When the infant gets older a complex environment would become attractive. The first part of this hypothesis seems to apply to the temporarily retarded development of IMR subjects concerning their distance from the mother. The IMR subjects may have been avoiding the adult conspecifics outside the separation cage. The second part of Rosenblum's hypothesis seems to be confirmed when at a later age the IMR subjects expanded their radius of action without the company of their mother. The IMR subjects then may have been attracted by the conspecifics outside.

Except for the retardation in range of action the IMR group did not differ much from the MMR group. The accessibility of the separation cage to peers and the company of another IMR subject (50% of the total observation period) seemed to be sufficient for the IMR group to equal the MMR group in social development. That MMR subjects had more social contacts with their mothers than IMR subjects may have been caused by hanging on another monkey's tail. This behaviour mostly was performed with the mother. In the separation cage the possibility to perform this behaviour was limited by the mother's custom to sit on the floor of the separation cage.

The time spent on exploration as a whole in both groups was constant during the whole observation period. The IMR and MMR subjects did not differ concerning the time spent on exploration despite the fact that the IMR subjects initially did not leave the separation cage. The IMR subjects came down to the floor, where most loose object were, at a later age than the MMR subjects did. This retardation in range of action is reflected in the finding that till the age of 20 weeks the IMR group spent less time exploring loose objects than the MMR group did.

Being carried about during the first months of life facilitates the development of the infant's range of action. This most probably is a result of getting familiar with the environment with the mother nearby. On the other hand being carried about by the mother is not necessary to get familiar with the environment as it appeared that IMR subjects finally began to move around independently. So the role of the mother in the development of self-reliant excursions by the young has to be considered as a catalyzing rather than as

an indispensable one.

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Chapter 5

The Range of Action of the Mother and the Avoidance of Big Novel Objects in Long-tailed Macaques

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Abstract. In previous studies we have found that most surrogate-reared long-tailed macaques persistently avoided a big novel object whereas most mother-reared subjects approached that object A striking difference between these attachment figures was that the mothers moved about with their infants whereas the surrogates were fixed to the wall Aim of the present experiment was to find out whether mobility of the attachment figure plays a part in the development of the infant's responses to big novel objects We studied the effects of mobility of the attachment figure by restraining mothers in their range of action Mothers of the experimental group were confined to a small part of the home cage The infants, however, could leave the cage in which their mothers were restrained Infants that were growing up with unrestrained mothers made up the control group. At two different ages all infants were exposed to a big novel object Two different objects were used We found that the range of action of the mother did not affect the responses of infants to big novel objects. Like found in the previous studies most of the mother-reared monkeys approached the objects The age at which an infant was first exposed to an object did not affect its behaviour towards that object. Further, the two different objects evoked the same reactions

Introduction

Rearing without a mother is known to produce excessive avoidance responses when subjects are confronted with novelty in chimpanzees (Menzel, et al., 1963; Menzel, 1964), in rhesus monkeys (Sackett, 1972), and in cebus monkeys (Elias & Samond, 1973). Timmermans et al. (1986) found that long-tailed macaques (*Macaca fascicularis*) reared on surrogate mothers in a peer group persistently avoided a big paper bag, whereas those reared by their mothers in a harem group approached that object. Röder et al. (1989a) confirmed this finding and concluded that the rearing condition and not the absence of an attachment figure during the first exposure to the object was the crucial factor in the development of this persistent avoidance behaviour (phobic behaviour). This behaviour was called phobic for reasons that: -the object was harmless; -the avoidance was persistent; the avoidance was maladaptive because food, near the object, was missed (see Timmermans et al., 1986; 1994).

The question which differences between surrogate and natural mother are responsible for this divergence in the reaction to big novel objects still has to be answered. Striking differences between a natural mother and an inanimate surrogate mother are the absence of responsiveness and mobility in the surrogate mother. For the normal development of the infant responsiveness as well as mobility of the attachment figure seem to be important. As responsiveness of the mother is very hard to manipulate (see Rosenblum & Pauly, 1984; Andrews & Rosenblum, 1991), it was decided to study the

effects of mobility.

To be carried through the environment by the mother could be an important element in the development of the young's explorative behaviour. The attachment figure serves as a secure base (Bowlby, 1977) from which the environment can be explored (King, 1966; Bronson, 1968), and to which arousal reducing qualities are ascribed (Baldwin & Baldwin, 1977). The mobility of the mother provides the young with the opportunity to explore the environment in the proximity of its attachment figure. So, in contrast with a young that is growing up with a static surrogate mother that it has to leave in order to explore the environment, a young reared by the natural mother can explore the environment within the range of action of the mother without leaving her proximity.

Restraining the mother in her range of action could affect the development of her infant's explorative behaviour: if the young stays near the mother it will not become familiar with the whole environment, and, if the young leaves the mother it will have to explore novel stimuli without her support.

Already we reported that restraining the mother in her range of action, while her young could freely move about, caused a retardation in the development of the young's range of action (Vochteloo et al., submitted). A parallel effect was found in surrogate reared monkeys (Duijghuisen et al., 1992). Young that from birth on regularly were moved through the cage on a mobile surrogate went farther away from their surrogates than young that grew up with static surrogates only.

The question now is whether rearing by restrained mothers retards the youngs' explorative behaviour directed at big novel objects, and whether these young are more prone to become phobic of big novel objects as Röder et al. (1989a) found in surrogate reared young.

To answer this question we restrained mothers in their range of action by placing them in a separation compartment inside the cage of the harem group they belonged to. Their young however could leave this separation compartment and enter the harem cage. The control group consisted of young of unrestrained mothers which both could freely move around in the same harem cage.

In our previous studies (Timmermans et al., 1986; Röder et al., 1989a) three

questions remained unanswered: did features of the novel object used, and the age of the first exposure play a part in the phobic reaction, and whether reaction to the object was affected by individual testing.

In our previous studies approach-avoidance behaviour was tested by exposing monkeys to only one object (a big paper bag) (Timmermans et al., 1986; Röder et al., 1989 a,b). It is possible that features of this object played a part in the development of the phobic behaviour. In the present experiment we wanted to establish whether object features played a role in avoidance behaviour by offering two clearly different big novel objects.

In Bronson's (1968) theory about the development of fear, three age-phases are distinguished. In the first phase novel stimuli do not elicit fear. In the second phase novel stimuli elicit fear which is reduced by the proximity of the mother. In the third phase the subject is able to approach novel stimuli independently. Röder et al. (1989a) exposed monkeys to the bag when they were in the second Bronsonian phase. So the age of the first exposure could have influenced the development of the monkey's reactions towards that big novel object. By using two ages of first exposure, offering one novel object in the second phase and another in the third phase, we tried to asses whether the reaction to a big novel object was affected by the age-phase in which the object was presented for the first time.

Röder et al. (1989a) tested by means of individual exposures. Monkeys, especially young ones, are disturbed by separation (Mineka & Suomi, 1978). It is possible that the response to separation played a part in the behaviour during tests. By alternating sessions with and without object we tried to discern separation effects and object effects. The sessions without object were used as control sessions.

Methods

Subjects and Housing

Eighteen long-tailed macaques (*Macaca fascicularis*) born in the laboratory and reared by their mothers were used as subjects.

The subjects and their mothers were members of harem groups of which there were three and which consisted of one male, four to nine adult females and a number of young between 0-3 years of age. The harem groups were housed in separate rooms in identical wire netting cages, measuring 4.0 x 3.8 x 2.0 m., which were divided in half by an opaque partition fitted with a sliding door (Fig. 1). Against the rear side of the left compartment of each cage, at the height of one meter, a wire-netting separation cage was constructed (1.3 x 1.0 x 1.0 m) (mesh width: 4 x 4 cm) that was used as housing for mothers of the experimental group. In the front side of the separation cage there was a slit in the netting through which young monkeys (but not adult ones) could pass.

The floor of the cages was covered with wood-chips. Some pieces of wood and a few plastic bowls served as toys. The monkeys were fed twice a day with Monkey-Chow (Hope farms). Additionally, pieces of apple and cereals were given once a week. Water was provided ad libitum through nipples. The lights were on from 8.00 till 20.00 hours.

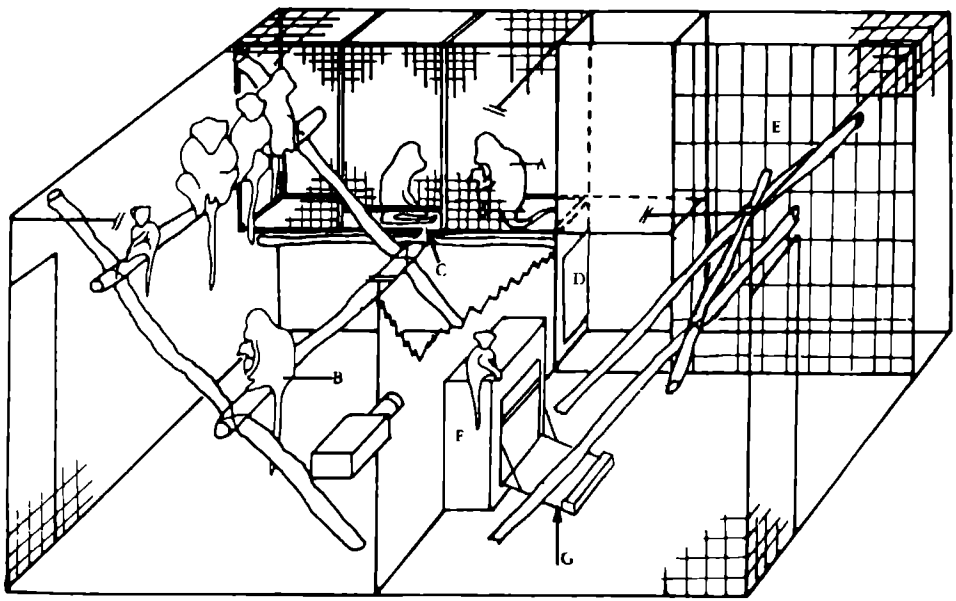

Fig. 1. *Harem-cage with experimental setup during sessions without object. A. restrained mother in the separation cage, B. unrestrained mother, C. slit in the netting, D. closed sliding door, E. start cage, F. presentation box, G. flap + apple feeding-device.*

Experimental setup

The experimental setup was permanently located in the right compartment of the cages. At the rear side a start cage was constructed (see Fig. 1).

Halfway against the partition there was a presentation box (1.2 x 1.0 x 0.35 m) which was used to present the novel objects. The front of this box consisted of a hinged flap which could be lowered. On the flap an object could be mounted. In front of the object, at the outer rim of the flap an apple feeding device was mounted. When the presentation box was open the object was exposed with an apple feeder in front of it. By means of this apple feeder pieces of apple could be presented. When there were no exposures or tests the box (without object) was open. As the subjects could move around freely, they were familiar with the experimental setup. The door of the start cage, the flap of the box, the apple feeder, and a video camera were under remote control.

Experimental design

The experimental design is presented in table 1.

The effects of four variables on the reaction to a big novel object were studied. These variables were: Rearing condition, Kind of object, Age of first exposure, and in order to discern effects of separation and effects of the object, Object presence.

Table 1. *Experimental design*

Rearing Condition [1]	Kind of Object	Age First Exposure	Age of Testing				Kind of Object	Age First Exposure	Age of Testing	
		months 6	7	12	18	24		months: 20	21	26
MMR (n=9)	bag(n=5)	3 sessions with object	alternately 3 sessions with object and apple, and 3 sessions with apple only				chair(n=5)	3 sessions with object	alternately 3 sessions with object and apple, and 3 sessions with apple only	
	chair(n=4)						bag(n=4)			
IMR (n=9)	bag(n=5)						chair(n=5)			
	chair(n=4)						bag(n=3) [2]			

[1] MMR= Reared with an unrestrained mother
IMR= Reared with a restrained mother

[2] one subject had died at the age of 19 months

At the age of 6 months all subjects were exposed to their first object for the first time. In both rearing-conditions 5 subjects were exposed to a bag and 4 subjects to a chair. Exposures consisted of three 30 minutes sessions with only the object. Tests took place at 7, 12, 18, and 24 months and consisted of three sessions with the object and pieces of apple and three 30 minutes sessions with pieces of apple only, alternately. At the age of 20 months all subjects were exposed to their second object for the first time. In each rearing-condition 5 subjects were exposed to the chair and 4 subjects to the bag. Tests took place at 21 and 26 months. The procedure for exposures and tests was the same as with the first object.

Rearing conditions

To determine the effects of range of action of the mother on the development of the ability to approach a big novel object, subjects grew up in one of two conditions:

1) with their mothers that freely could move around in a harem cage (Mobile Mother Reared = MMR),

2) with their mothers that were housed in separation cages within a harem cage (Immobile Mother Reared = IMR).

All subjects were born between January 1988 and August 1990. The MMR group consisted of 7 females and 2 males, and the IMR group of 3 females and 6 males.

MMR and IMR subjects lived in the same harems. In order not to disturb the social structure of a harem group we had to take into account that in each harem group at the same time only two mothers could reside in the separation cages. This way of assigning the mothers caused an unbalanced sex ratio in the two groups of subjects, but in our previous studies no relation between sex and persistent avoidance behaviour had appeared (Röder et al., 1989a).

A subject of the IMR group was put into the separation cage with its mother within two days after birth. The mother had to stay in the separation cage for one year. A mother of an IMR subject always had company of another adult female with or without an infant. Thus the separation cage always was occupied by two females and one or two subjects of the IMR group.

Kind of object

To determine whether object features affected avoidance behaviour, two objects of approximately the same size but of different shape, colour, and material were used: a blue paper bag, measuring 72 x 45 x 15 cm. (like Röder et al., 1989 a,b used), and a yellow wooden chair-like construction measuring 65 x 45 x 45 cm.

Age of first exposure

To determine whether the age at which a novel object is first presented plays a role in the subject's reaction to that object, first exposures were carried out at two ages. The subjects were first exposed to an object at the age of 6 months. At this age the subjects were supposed to be in the second Bronsonian phase (Bronson, 1968). At the age of 20 months the same subjects were first exposed to the other object. At this age they were supposed to be in the third Bronsonian phase. A number of subjects got the bag at 6 months and the chair at 20 months, the other subjects got the reversed order.

At this point the experimental design is biased. A correct design should evade effects of experience with the first object on the behaviour towards the second object. Therefore one group should be exposed only at 6 months and the other group only at 20 months. Monkeys are scarce, however, and we took a chance on the outcome. In case animals become phobic only of the first object this would indicate that the phobia we are studying develops during the second Bronsonian phase and is restricted to the object then presented. In case animals become phobic of both objects or of only the second no conclusions can be drawn.

Object presence

In order to determine the effect of the object on the behaviour of the subject test sessions with object were alternated with test sessions without object. During a test series sessions 1, 3, and 5 were carried out without object and test sessions 2, 4, and 6 with object.

To discern effects of separation and of the object, and to make sure avoidance of the object could not be ascribed to lack of interest, during all test sessions 5 pieces of apple were presented on the flap of the presentation box by means of the apple feeder.

Procedure

Before each session all monkeys were driven into the left compartment. Then the experimental setup was prepared. In case of first exposure only the object was mounted on the flap of the presentation box. The subject to be tested was driven into the start cage while the other monkeys stayed in the left compartment and the sliding door between the compartments was closed. After a period of 30 minutes to quiet down the session was started by lowering the flap of the presentation box and opening the start cage. During 30 minutes the behaviour of the subject was recorded on video. The session was finished by closing the presentation box and opening the sliding door between the compartments. All first exposures and test series were carried out with intersession intervals amounting to 24 or 48 hours.

Parameters

During all test sessions the subjects' behaviour and location were continuously registered from the video recordings. The parameters are presented in table II.

Statistics

For each test series the data of the three sessions without and of the three sessions with an object were pooled separately for each parameter. The mean values were used in the analyses.

Concerning the object first exposed at 6 months the effects of "sex" and "kind of object" were analyzed by means of a MANOVA. As no parameters were affected by "sex" and "kind of object" they were further analyzed by means of a MANOVA with "rearing condition" as between subject factor and "object presence" as within subject factor.

Whether "rearing conditions" had an effect on the number of subjects that approached the object (approacher) was analyzed by means of the Fisher Exact Probability test. A subject was called an approacher if in the course of a test series during sessions with an object it took more than one piece of apple, or sat more than once on or next to the flap of the presentation box during more than one 5 s period, or touched the object more than once.

Table 2. *Parameter Definitions*

Parameter	Definitions	Reproduced as
Behaviour		
locomotion	moving at least on body length	% time
autoactivity	grooming, sucking and manipulating own body parts	% time
attentivity	looking in a certain direction, while in a tense posture	% time
manipulation flap	touching the flap of the box or the apple feeder with hand or mouth	sec
manipulation object	touching the object with hand or mouth	sec.
taking apple	taking a piece of apple from the apple feeder	n
eating apple	eating pieces of apple from the apple feeder	sec.
other	behaviour not defined above	% time
Location		
start cage	inside the start cage	% time
ground	on floor, "start cage" and "near flap" excluded	% time
lower part	area up to 1 m high, "ground" and "start cage" excluded	% time
upper part	area above 1 m, "start cage" excluded	% time
near flap	on the floor with 40 cm of the flap of the presentation box	sec
on flap	on the flap of the presentation box or on the object	sec

In order to find effects of the age of first exposure the data obtained with the objects first exposed at 6 months were compared with the data obtained with the objects first exposed at 20 months. First, by comparing the first test series after the first exposure i.e. the test series at 7 and 21 months, and second by comparing the test series taken at about the same age, i.e. the test series at 18 and 24 months versus the test series at 21 and 26 months. The number of approachers was compared by means of a Fisher Exact Probability test. The analyses of the behaviour and of location were performed by means of a MANOVA with "rearing condition" as between subject factor and "age of first exposure" and "object presence" as within subject factors.

Results

Sex

There were no sex effects when the overall means of all test series were compared. A comparison for each series of tests separately showed only one significant difference. At the age of 7 months females spent more time on locomotion than males ($F_{1,11}$= 5.11, p< 0.05).

Kind of object

The kind of object (bag or chair) made no difference whatsoever.

Table 3. *Numbers of subjects taking more than one piece of apple near the object and/or sitting more than once on the flap of the presentation box near the object for more than 5 s and/or touching the object more than once, per test series, for all test series, and, the total numbers of subjects (Σ) that fulfilled these criteria during one or more test series.*

			Age of testing (months) with object first exposed at 6 months							Age of testing (months) with object first exposed at 20 months		
Rearing Condition [1]	Kind of Object		7	12	18	24	Σ	Kind of Object		21	26	Σ
MMR (n=9)	bag	(n=5)	1	2	3	3	3	chair	(n=5)	3	5	5
	chair	(n=4)	1	3	3	3	4	bag	(n=4)	3	1	3
IMR (n=9)	bag	(n=5)	2	2	4	5	5	chair	(n=5)	4	5	5
	chair	(n=4)	2	3	4	3	4	bag	(n=3)	3	1	3

[1] MMR= Reared with an unrestrained mother
IMR= Reared with a restrained mother

Rearing condition

A comparison of the rearing conditions, for each series of tests separately showed that rearing condition had no effect on the number of approachers (Fisher Exact Probability test; p> 0.21) (see Table 3).

Table 4. *Mean results (± SEM) of test series concerning the object first exposed at the age of 6 months.*

Parameters	Rearing Condition [1]	Object Presence [2]	Age of Testing				F-Values [3]	
			7 months	12 months	18 months	24 months	Rearing Condition	Object Presence
Number of Pieces of Apple Taken	MMR	-	2.9±1.3	7.9±1.8	9.8±1.3	8.9±1.4	0.58	38.3**
		+	0.8±0.7	3.3±2.0	4.9±2.1	4.9±2.0		
	IMR	-	2.9±1.3	5.9±1.6	7.9±1.9	6.0±1.5		
		+	2.3±1.1	2.8±1.1	3.0±1.4	3.8±1.8		
Manipulation Flap (sec)	MMR	-	5.6±2.7	15.3±2.8	8.4±2.6	8.2±4.1	0.26	8.19*
		+	3.7±2.9	8.7±3.1	5.8±2.9	3.6±2.6		
	IMR	-	4.9±3.2	9.1±3.0	12.6±5.4	2.9±1.1		
		+	6.3±3.7	4.8±1.6	8.3±3.3	1.9±0.9		
Ground (%time)	MMR	-	8.6±2.1	16.2±2.8	20.3±3.5	17.6±5.5	0.17	2.35
		+	9.9±2.6	17.2±3.4	15.8±2.8	17.2±5.4		
	IMR	-	7.2±1.3	10.9±1.5	21.8±2.0	18.4±5.3		
		+	6.6±1.7	10.2±2.2	20.1±2.5	16.7±6.0		
Near Flap (sec)	MMR	-	65.2±32.3	111±28	185±46	193±73	0.00	2.23
		+	60.7±35.2	138±55	153±48	185±74		
	IMR	-	53.2±17.7	74.2±19.3	235±60	250±91		
		+	44.3±15.7	84.7±27.3	197±65	107±64		
On Flap (sec)	MMR	-	49.4±33.9	71.0±14.7	59.9±12.0	51.9±15.1	0.18	20.1**
		+	1.6±1.3	6.0±4.3	9.1±4.5	2.9±1.9		
	IMR	-	22.4±10.6	53.9±24.7	65.1±19.5	27.0±16.9		
		+	21.0±13.7	10.4±4.8	9.6±5.7	0.4±0.3		

[1] MMR = Reared with an unrestrained mother in a harem
IMR = Reared with a restrained mother in a harem

[2] - sessions without object
+ sessions with object

[3] * $p < 0.05$
** $p < 0.01$

As table 4 shows the IMR and the MMR group did not differ in any reaction towards the big novel objects. Also concerning the other parameters there were no differences between the two rearing conditions ($F_{1,15} < 2.28$, ns).

In the course of the test series the number of pieces of apple taken ($F_{3,45} = 10.1$, $p<0.01$), the time spent on manipulating the flap ($F_{3,45} = 8.46$, $p<0.05$), the time spent near the flap ($F_{3,45} = 8.46$, $p<0.01$), and the percentage of time spent on the ground ($F_{3,45} = 7.44$, $p<0.01$) increased.

Age of first exposure

Table 3 shows that the number of approachers during the test series at 7 months (first object) is lower than during the test series at 21 months (second object) (Pearson's Chi Square= 6.56, $p= 0.011$). A comparison of the number of subjects approaching the first and the second object at about the same age (18 and 24 months versus 21 and 26 months) did not reveal effects of age of first exposure (Pearson's Chi Square= 0.31, $p= 0.58$). In the course of successive test series the number of subjects that approached the first object increased from 6 to 14 (Pearson's Chi Square= 8.58, $p= 0.0034$). Subjects approaching the first object at the age of 18 and 24 months also approached the second object. In the MMR group there were three exceptions to this rule; two subjects avoiding the first object, approached the second object during the test series at 26 months, and one subject approaching the first object during the test series at 18 and 24 months avoided the second object during the test series at 21 and 26 months.

Concerning behaviour and location a comparison of the results of the test series at 7 months with the test series at 21 months, and, of the results of the test series at 18 and 24 months with the results obtained at 21 and 26 months, revealed no differences.

Object presence

During sessions with object less pieces of apple were taken than during sessions without object ($F_{1,15} = 38.3$, $p< 0.01$). When the object was present less time was spent on manipulating the flap of the presentation box and sitting on it than during sessions without object (respectively; $F_{1,15} = 8.19$, $p< 0.05$; $F_{1,15} = 20.1$, $p< 0.01$) (see Table IV).

Even when approachers are considered separately less pieces of apple were taken

and less time was spent on manipulating the flap, and sitting on it during sessions with object than during sessions without object (respectively; $F_{1,13}= 29.4$, $p< 0.01$; $F_{1,13}= 5.02$, $p< 0.05$; $F_{1,13}= 19.5$, $p<0.01$).

Discussion

Röder et al. (1989a) found that most monkeys reared with immobile surrogate mothers were phobic of a big novel object (a bag) whereas most monkeys reared with their natural mothers, that could freely move about in the harem cage, were not. Which difference between mother-rearing and surrogate-rearing was relevant to explain the difference between mother-reared and surrogate-reared young? From the views of King (1966), Bronson (1968), Baldwin and Baldwin (1977, 1978) and Bowlby (1977), who claim that early in life the immediate proximity of an attachment figure enhances the development of exploratory behaviour of the infant, we deduced the hypothesis that lack of support by the mother during excursions in the environment would impede the development of infant's ability to independent approach towards big novel objects. The main purpose of the present experiment was to study the effects of a restricted range of action of the mother during the first year of life of the infant, on the infant's response to big novel objects.

Already we reported that, during the first half year, young of restrained mothers only rarely had ventro-ventral contact with other, free moving, adults and they did not differ from young of unrestrained mothers in this contact (Vochteloo et al., 1993). So it seem improbable that other free moving adults served as a secure base and obliterated eventual effects of the mothers' restraint. Although the development of the range of action of young growing up with a restrained mother indeed was retarded (Vochteloo et al., submitted), their reaction to big novel objects did not differ from the reaction of young that grew up with mothers that freely moved about. The retardation in the development of the range of action in subjects growing up with restrained mothers played no part at all during individual confrontations with a big novel object; already during the first test series 4 out of 9 IMR subjects approached the object. Apparently Röder et al.'s (1989a) finding

that most surrogate-reared monkeys were phobic and most mother-reared were non-phobic was not caused by the difference in range of action between a surrogate and a real mother.

We used the same test procedures as Röder et al. (1989a) did and our results concerning the behaviour towards novel objects, the percentage of subjects approaching the objects, the absence of sex differences, and the increase of the number of subjects approaching the objects did not differ from Röder et al.'s findings with subjects reared with their unrestrained mothers. We will return to the question of relevant differences between mother and surrogate rearing later on.

Though the novel objects finally were approached by most subjects, the presence of the objects kept affecting their behaviour. After they had sufficiently overcome the effects of separation to take pieces of apple during test without the object, they still reacted to the presence of the object by taking fewer pieces of apple, and by spending less time near the presentation box. So it seems that, although the object brought about avoidance reactions, the subjects were able to cope with the tendency to avoid the objects.

In previous studies (Röder et al., 1989 a,b; Timmermans et al., 1986) only one object was used, a big paper bag. Therefore it could not be excluded that the persistent avoidance behaviour depended on features of this object. The outcome of the present experiment is that the number of approachers was equal for both objects and the groups also did not differ in other behavioural parameters. This result corresponds with the findings of Vochteloo et al. (1991) that monkeys that were phobic of the bag also were phobic of two other big novel objects, presented to them successively, and that monkeys that approached the bag also approached these two objects. Timmermans et al. (1986) argued that the phobic reaction to a novel object could have been acquired as a consequence of exposure to that novel object during the second phase of the development of fear (Bronson, 1968) in absence of the attachment figure. Already we reported that the presence or absence of the mother during the first confrontation did not affect the number of subjects approaching the big novel object (Röder et al., 1989). The findings of the present experiment showed that monkeys which were confronted with novel objects without the mother presence, finally behaved the same way whether tested with objects first presented at 6 months or at 20 months. These results confirm the results of Vochteloo et al. (1991) who found that monkeys reacted to big novel objects first presented at the

age of 31 and 42 months in the same way they had reacted to the bag which was presented much earlier. Therefore it can be concluded that the phobic behaviour was not restricted to objects first exposed during the second phase of the development of fear. Contrary to King's (1966) suggestion it appeared that subjects were capable of approaching objects although these were exposed to the subjects in absence of their mothers.

Our data show that there was a gradual decrease in the number of subjects avoiding the object. As all subjects got a series of successive tests, conclusions concerning the question whether the decrease in the number of avoiders was caused by accumulating experience with the object or by developmental changes not affected by experience with the object, can not be drawn.

We now return to the question of the relevant difference between mother and surrogate rearing.

Mason & Capitanio (1988) found that young rhesus monkeys reared on an animate surrogate mother (a dog) were more explorative than those reared on an immobile lifeless surrogate and suggested that the positive effect of the animate surrogate was due to response contingent stimulation it provided. Mineka et al. (1986) found a positive effect on explorative behaviour and a decline in fear responses in rhesus monkeys which, during their development, had the opportunity to control food and water provisions. Whether lack of response contingent stimulation during surrogate-rearing plays a part in the development of the ability of young monkeys to approach big novel objects can be studied by rearing monkeys with surrogates in conditions in which they can learn to have control over environmental stimuli.

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Chapter 6

The Development of Explorative Behaviour in Long-tailed Macaques (*Macaca fascicularis*) Reared with Their Mothers and Peers: A Pilot Study

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In a study by Röder et al. (1989) it was found that most surrogate-reared monkeys (*Macaca fascicularis*) avoided a big novel object whereas most mother-reared subjects did not. Differences between the attachment figures, e.g. mobility and responsiveness, might have caused this disparity. Another difference between the two rearing conditions, however, might have played a part. In addition to their mothers and peers the mother-reared subjects had a number of other (sub-)adult cage mates. The surrogate-reared subjects on the other hand only had peers as cage mates.

In young monkeys the presence of conspecifics benefits the development of social play, and of explorative behaviour, which are seen as important for adult functioning (see e.g. Dolhinow & Bishop, 1970; Higley & Suomi, 1986; MacDonald, 1986; McGrew, 1977; Poirier et al., 1978; Simonds, 1974; Welker, 1971). During the first months of life the presence of other adults can prolong the time a young has contact with its mother (Castell & Wilson, 1971; Hinde & Spencer-Booth, 1968; Kaplan, 1972; Wolfheim et al., 1970). When the infant grows older the presence of adults other than the mother can affect the development of independence; infants growing up with their mothers in the presence of other adults went farther away from their mothers than infants growing up alone with their mothers (Hinde & Spencer-Booth, 1968; see also Rosenblum, 1971). Further, adult conspecifics, as a source of environmental stimulation, might affect the behavioural development of the young. Jensen et al. (1968) reported that compared to monkeys reared in a stimulus-rich environment, monkeys reared in a stimulus-poor environment showed some retardation in their development of explorative behaviour and were less independent (see also Lee, 1986).

The aim of this study was to observe and describe the behavioural development and the reactions towards a big novel object of young monkeys that grew up with mothers that were restrained to a part of the cage. No other adults monkeys were present in this cage. In the discussion the results of this study are compared with the results from the

study of young that grew up in harems (Röder et al., 1989; Vochteloo et al., 1994a,b). The rearing condition only differs from surrogate rearing with regard to the characteristics of the attachment object: mother versus surrogate. In both conditions the attachment object does not support the young when it explores the cage. Therefore the results also will be compared to results of studies of the development of young that grew up on surrogates (Röder et al., 1989; Duijghuisen et al., in prep; Timmermans et al., 1994).

Methods

Subjects and Housing

The group consisted of six monkeys (4 females, two males), growing up with their mothers[1] that were individually housed in wire-netting separation cages (0.6 x 0.6 x 1.0 m). The separation cages were placed at a height of one meter in the rear part of the cage that measured 4.0 x 2.0 x 2.0 m. The separation cages had a slit in the netting through which only young monkeys could pass. Apart from the subjects and their mothers there were no other monkeys present.

Housing and maintenance was equal to previous experiments (Vochteloo et al., 1991, 1993, 1994 a,b).

1. Development

The development of the range of action and of some behaviours was assessed. The range of action was measured in terms of the distance between the subject and the separation cage of its mother, and the time spent in the separation cage, in the front and rear part of the cage, and on the floor.

The behavioural parameters are presented in table 1.

[1]In the course of experiments in which the effects of restriction of mother's radius of action were studied we obtained some adult female monkeys that had been used for breeding in another institute. These monkeys were accustomed to individual housing. We used this opportunity for the present pilot study of the effects of growing up in the absence of other adults on the development of explorative behaviour.

Table 1. *Parameters recorded during the observations of behavioural development.*

Behaviour	Definition
Autoactivity	grooming, sucking and manipulating own body parts
Locomotion	moving at least one body length
Exploration	manipulation of objects; a distinction was made between loose objects (e.g. wood chips, toys) and fixed objects (e.g. climbing poles, wire)
Social behaviour	physical interaction with a conspecific
Other	behaviours not defined above

Observations

Subjects were observed once a week for half an hour from 6 until 26 weeks of age and once a fortnight from 27 until 41 weeks of age. In the 50-th week the subjects were observed once for one hour and a half. The observation periods were randomly scheduled across the week between 09.00 and 17.00 hours. Because the wall of the separation cages prevented reliable observations inside the separation cages only the activities outside the separation cages could be observed. During all test sessions the subjects' behaviour and location were continuously recorded on video and thereafter registered on an event recorder.

2. Reactions to a big novel object

In order to determine whether there is an effect of growing up in the absence of other adults on the subjects' ability to approach big novel objects the subjects were exposed to a big novel object. The object was the same as used in previous experiments (Vochteloo et al., 1991; 1994b); a blue paper bag. At the age of 6 months the subjects were individually exposed to the bag. At the age of 7, 12, 18, and 24 months the subjects were tested individually with this object. The first exposures to the object consisted of three sessions of 30 minutes with intervals amounting to 48 hours. In order to distinguish object effects from separation effects three test sessions with object were alternated with

three sessions without object. To be sure that avoidance of the object could not be ascribed to lack of interest pieces of apple were offered during all test by means of an apple feeding device in front of the object. Similar to exposure sessions, test sessions lasted 30 minutes. The interval between test sessions amounted to 24 hours.

Set-up

For the purpose of exposures and tests the cage could be divided into two compartments by an opaque partition: front and rear part. The experimental set-up was located in the front part, the separation cages in the rear part. The device to present novel objects was permanently located in the front part. It consisted of a hinged flap which could be lowered and on which an object and an apple feeding device could be mounted. By means of this feeder pieces of apple could be presented. When the flap was in the lowered position the object was exposed with the apple feeder in front of it. When there were no exposures or tests the flap (with apple feeder, without object) was in the lowered position.

At the right side of the front part, against the wall, a start cage was constructed.

As the subjects could move around freely, they were familiar with the experimental set-up. The apple feeder was regularly used to feed pieces of apple to the whole group of subjects. The door of the start cage, the flap, the apple feeder, and, a video camera were under remote control.

Procedure

Before each session the partition dividing the cage in two parts, was closed. Then the set-up was prepared.

In case of first exposure sessions only the object was mounted on the flap. In case of test sessions without object (sessions 1, 3, and 5) 5 pieces of apple were put into the feeder, and in case of test sessions with object (sessions 2, 4, and 6) the object and 5 pieces of apple were put into position.

After this the flap was closed. The subject to be tested was driven into the start cage. After a period of 30 minutes for the subject to quiet down, the session was started by lowering the flap and opening the start cage. The five pieces of apple were offered

with intervals of 6 minutes. After the session was finished, the partition was opened.

Table 2. *Parameters recorded during exposures to a big novel object.*

Parameter	Definition	Reproduced as
Behaviour		
Manipulation flap	touching the flap of the presentation box or the apple feeder with hand or mouth	sec.
Manipulation object	touching the object with hand or mouth	sec.
Taking apple	taking a piece of apple from the apple feeder	n
Eating apple	eating pieces of apple taken from the apple feeder	sec.
Location		
Ground	on floor, "near flap" excluded	% time
Near flap	on the floor within 40 cm of flap of the presentation box	sec.
On flap	on the flap of the presentation box or on the object	sec.

Parameters

In order to assess the reactions to the object and to distinguish the effects of separation from the effects of the object, the parameters, presented in table 2, were scored.

Statistics

1. Development

The data were divided into age-blocks of 28 days and expressed in percentages of time "out of separation cage". The means of the age-blocks were polynomially transformed and subsequently analysed using a MANOVA trend analysis procedure with age as within subject factor. In the figures presented a second order polynomial curve was fitted.

2. Reactions to a big novel object

For each test series the data of the three sessions without and of the three sessions with object were pooled separately for each parameter. The mean values were used in the

analyses.

In order to distinguish the effects of the object from separation effects, the sessions without and the sessions with object were included in the analyses as within subject factor "object presence". The data were analyzed by means of a MANOVA trend analysis procedure.

To determine the number of subjects that approached an object a subject was called an approacher if in the course of a test series during the sessions with an object it took more than one piece of apple, or sat more than once on or next to the flap during more than one 5 s period, or touched the object more than once.

Results

1. **Development**

Behaviour

The percentage of time the subjects spent on exploration of loose objects increased (Flin(1,5)=15.2, p=0.011), whereas during that same period the percentage of time spent on

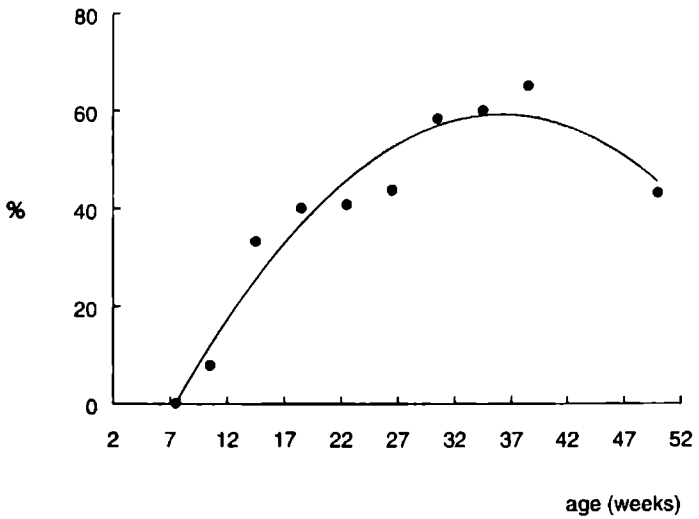

Fig. 1. *Mean percentage of the observation time (± SEM) (per period of 28 days and second order polynomials) that subjects were out of the separation cages.*

exploration of fixed objects decreased (Flin(1,5)=24.9, $p< 0.01$). The total percentage of time spent on exploration did not change during the course of the observation period.

The percentage of time spent on locomotion, social and autoactive behaviour did not change during the observation period.

Range of action

In the first age block (6 - 10 weeks) the subjects rarely left the separation cages. After that the time the subjects were out of the separation cages increased (Flin(1,5)=76.7, p<0.01) (see Fig. 1). When out of the separation cages the subjects spent more than 50% of their time within 0.5 m from the separation cages (see Fig. 2). The time the subjects spent at a distance between 0.5 - 1.5 m from the separation cages increased from about 1% (age 10 weeks) till about 40% (age period 32-50 weeks) (Flin(1,5)=55.4, $p< 0.01$). The subjects hardly came beyond 1.5 m from their mothers' separation cage (only in age block 9, age 38 weeks, more than 10%, other age blocks between 3% and 8%). The time subjects spent at more than 1.5 m increased (Flin(1,5)=43.9, $p< 0.01$).

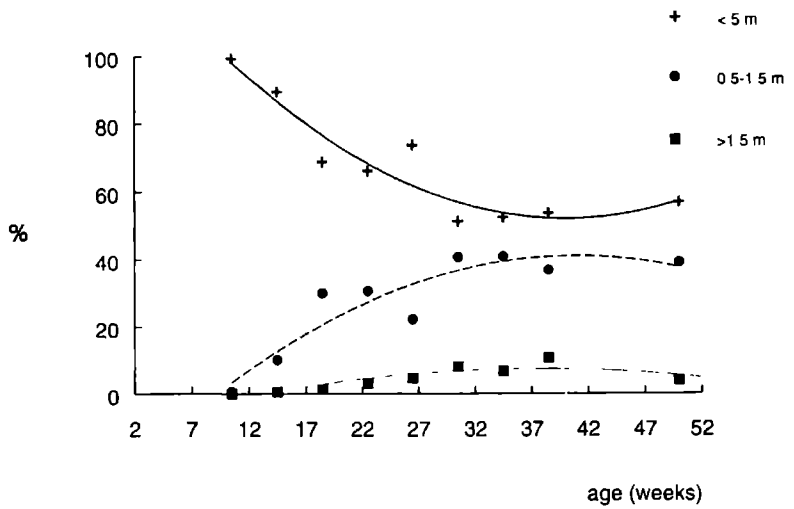

Fig. 2. *Mean percentage of the time out of the separation cage (per period of 28 days and second order polynomials) that subjects stayed at distances of less than 0.5 m (+), between 0.5-1.5 m (●), and more than 1.5 m (■) from their mothers' separation cage.*

This limited range of action also became clear from two other parameters: the time spent on the floor and in the front of the cage. During most observation sessions subjects spent about 4% - 8% of the time on the floor. Further they spent about 80% - 90% of the time in the rear part, about 5% - 20% in the middle part, and the rest (varying between 0% - 5%) of their time in the front part of the cage. During the observation period the time the subjects spent on the floor increased ($F_{lin(1,5)}=31.5$, $p< 0.01$).

2. Reactions to a big novel object

Object presence

During one or more tests three out of six subjects approached the object. More pieces of apple were taken during the sessions without the object than during sessions with

Table 3. *Mean results (± SEM) of test series with and without object.*

Parameters	Object Presence [1]	Age of Testing			
		7 months	12 months	18 months	24 months
Number of Pieces of Apple Taken	-	1.2±0.5	1.3±0.3	0.3±0.3	4.3±1.7
	+	0	0.3±0.2	0.5±0.3	2.2±2.2
Manipulation Flap (sec)	-	4.2±2.0	14.2±4.1	3.3±2.0	1.7±1.1
	+	4.0±3.6	9.7±4.9	2.2±1.5	3.6±3.6
Ground (%time)	-	8.3±2.9	13.8±2.6	12.8±6.2	6.3±3.4
	+	8.0±3.2	14.0±3.1	11.7±5.2	4.3±2.4
Near Flap (sec)	-	56.0±33.3	65±28	120±101	107±64
	+	51.0±42.0	55.5±33.5	80.3±60	71.3±45.6
On Flap (sec)	-	25.3±12.1	37.3±16.2	54.7±35.5	5.5±4.0
	+	8.0±7.6	25.8±24.4	37.7±34.9	0

[1] - sessions without object
+ sessions with object

the object ($F(1,5)=12.76$, $p=0.016$). Concerning the other parameters there were no differences between the sessions with and without the object (table 3).

In the course of successive test series only the time spent on manipulating the flap increased ($F(3,15)=3.83$, $p=0.032$).

Discussion

It appeared that monkeys that grew up with a restrained mother without other adults rarely left their mothers' separation cages until the age of 10 weeks. Thereafter they mostly stayed within 1.5 m from it. Further it appeared that three out of six subjects approached a big novel object.

Before comparing the results of this pilot study with results obtained in studies with mother-rearing in a harem and surrogate-rearing in a peer group, we will pay attention to some other factors that, next to the absence of other adults, may have influenced the subjects' development.

Castell & Wilson (1971) and Kaplan (1972) reported that mothers housed in a restricted environment without other conspecifics rejected and avoided their infants more than mothers housed in a social group. According to Kaplan this enhanced punishment and avoidance by the mother was due to the increase in the number of contacts made by the infant; this increase was due to lack of opportunity for the infant to make social contact with other conspecifics (Kaplan, 1972; see also Rosenblum, 1971, pp. 355). In contrast with the conditions mentioned, the infants in our set-up could and did leave the separation cage of their mothers and did make social contacts with other conspecifics. If these mothers had been more rejective, the infants probably had shown a larger radius of action, since it has been found that infants of more rejective mothers have a greater radius of action than infants of less rejective mothers (baboons: Altmann, 1980; rhesus monkeys: Hinde & Spencer-Booth, 1968).

Another factor that may have played a role was that mothers were solitarily housed during pregnancy. This solitary housing may have affected the subjects' behaviour. Schneider (1992) compared young of mothers that were exposed to stressful noise bursts

during pregnancy with young of mothers that were not exposed to these stimuli. She found that in a novel environment young of mothers that had been exposed to noise bursts exhibited more disturbed behaviour (clinging and self-directed behaviour) and less exploratory behaviour than the control subjects. Although we did not see disturbed behaviour during our observations, we can not rule out that the housing condition of the mother was stressful.

Nevertheless it seems worthwhile to compare the results of the present pilot study with the results of related experiments.

Vochteloo et al. (1994a) found that monkeys that were reared by restrained mothers in a harem spent more time in proximity of their mothers and used a smaller part of the cage than infants reared by unrestrained mothers during the first half year of their lives. However, after the first 6 months their radius of action increased and after one year their arrears had been overcome. The young in the present study, growing up with restrained mothers in the absence of other adults stayed in the proximity of their mothers (within 1.5 m from their mothers' separation cage) up to 1 year of age. Therefore, it seems that before the age of one year young do not take the initiative to visit places if there are no other monkeys at those places. When young begin to move independently from their mothers other conspecifics begin to fulfill a role as consort. Their presence facilitates the young to visit places where these conspecifics are.

Peers are especially attractive to be followed by young monkeys (see Dolhinow & Bishop, 1970) but youngs' activity greatly depends on the presence of adults. It needs no argument that the tendency of infants to stay near adults is adaptive in the natural habitat. If other adults are absent each individual young stays near its restrained mother and the other restrained mothers in the rear part of the cage.

Growing up in a peer group with restrained mothers in the absence of other adults resembles growing up in a peer group with surrogate mothers. In both conditions young have to venture away from their attachment figures without the assistance and facilitation that may be provided by the presence of the other adults. Duijghuisen et al. (1992) found that monkeys reared in peer groups with surrogate mothers that were fixed against the wall, showed a retarded development of their radius of action when compared to monkeys growing up in peer groups with surrogate mothers that were moved through the cage.

In view of the finding that half the number of subjects reared by restrained mothers in absence of other adults approached a big novel object, it seems that their reaction towards the object is somewhere between the reaction of surrogate-reared and mother-reared subjects.

If we compare the results concerning tests with a big novel object with the results obtained with monkeys reared by their mothers in a harem and monkeys reared in a peer group with surrogate mothers it appears that most monkeys (82%) reared by their mothers approached big novel objects (Röder et al., 1989; Vochteloo et al., 1994b) whereas most monkeys (84%) reared on surrogate mothers avoided these objects (Röder et al., 1989; Duijghuisen et al. in prep; see Timmermans et al., 1994 for a review).

Another interesting finding in the present study was that the subjects took few pieces of apple (average: 1.7) during sessions without the object. Monkeys reared in a harem on the average took 6.5 pieces of apple in sessions without the object (Vochteloo et al., 1994b). This "taking apple" behaviour of subjects reared by restrained mothers in absence of other adults resembles the behaviour of monkeys reared on surrogate mothers; they also took few pieces of apple during tests without object. Röder et al. (1989) reported that up to the age of 16 months 5 out of 12 surrogate-reared and 11 out of 12 mother-reared monkeys took pieces of apple during sessions without the object. Duijghuisen et al. (in prep), using the same surrogate-reared procedure as Röder et al., found that only 1 out of 9 subjects took pieces of apple during sessions without the object. This reluctance to take apple may indicate that the capability to cope with separation was reduced.

In general it seems that if the mother is not capable to accompany and support the infant exploring the environment and other conspecifics are absent, the infant's development seems to be retarded. If this is true, being cared for by a biological mother does not completely compensate for the deficiencies of surrogate rearing, when the development of explorative behaviour is at stake.

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Chapter 7

General Discussion

In her study concerning the effect of rearing conditions (natural mother versus surrogate mother) on the development of phobic behaviour in long-tailed macaques, Röder (1990) concluded that the chance to develop a phobia was significantly enlarged by growing up with a surrogate mother.

My follow up study involved three questions concerning the phobic behaviour in long-tailed macaques: the first question concerns the characteristics of the phobic behaviour, and the other two concern the relevant differences from the rearing conditions studied by Röder, namely the mobility of the mother and the absence of adult monkeys other than the mother.

Concerning the characteristics of the phobic behaviour it was questioned whether the avoidance behaviour was restricted to the paper bag that was used by Timmermans et al. (1986) and Röder et al. (1989) or other novel objects were avoided as well. In case only the bag was avoided, the behaviour would resemble a simple phobia, and in case other novel objects also were avoided, we would be dealing with a neophobia.

In the first experiment (chapter 2) the original object (the bag), two big novel objects, and four small novel objects successively were presented to monkeys of which it was known that they formerly approached or avoided the bag. Again it appeared that although the surrogate-reared monkeys had been confronted with the bag several times, and they meanwhile became "familiar" with this object, they kept avoiding it. This behaviour confirms the persistence of the avoidance behaviour. Further it appeared that monkeys that avoided the bag also avoided other big novel objects, and that monkeys that approached the bag also approached other big novel objects. Small novel objects were approached by all subjects. So, shape of the objects was of no importance, while, in case monkeys were phobic, the size of the object affected their behaviour.
Menzel (1962) also concluded that size is a prepotent determinant of responses to an object. He found that in rhesus monkeys big objects evoked more avoidance behaviour than small objects.

In another experiment (chapter 5) the characteristics of the phobic behaviour were

studied again. Instead of successive presentation of big novel objects, like in the first experiment, this time, at the age of 6 months, monkeys of one group were confronted with a bag and monkeys of another group with a chair. Again it appeared that shape of the object did not play a part in the reactions it evoked. Also Duijghuisen et al. (in prep) found that in surrogate-reared monkeys the shape of the object did not determine the subjects' reactions. So it appeared that the reaction of mother- and surrogate-reared monkeys towards big novel objects was not determined by the shape of the object.

Whether the age at which a subject was exposed to a big object for the first time played a role in the reaction towards that object was studied by confronting the same group of monkeys with another big novel object at the age of 20 months. It appeared that the reactions of the subjects towards a big object did not depend on the age at which they were exposed to that object for the first time. Also in monkeys reared with surrogate mothers it was found that the age of first exposure did not determine the reaction towards that object (Duijghuisen et al., in prep). In view of the results of the first (Vochteloo et al., 1991) and the second experiment (Vochteloo et al., 1994) it seems that the age at which a subject is confronted with a big novel object is not decisive for the occurrence of avoidance or approach. Generalization, due to the test-procedure we used, can be excluded because in the first experiment monkeys did not avoid small objects although the test-procedures for big and small objects were identical. (see also Timmermans et al., 1994 about context conditioning). However, generalization restricted to big objects can not be excluded. In order to exclude this one has to confront surrogate and mother reared monkeys for the first time with a big novel object at two different ages.

The fact that all subjects approached small novel objects and that neither the shape of the objects nor the age at which a subject was confronted with a big novel object for the first time had an effect on the reactions towards the object leads us to the conclusion that we are dealing with a neophobia of big novel objects.

Neophobic reactions already were reported to occur in rats (Barnett & Cowan, 1976). These authors concluded that rats avoiding one novel object generally avoided other novel objects as well (avoiders), whereas rats approaching one novel object also approached other novel objects (non-avoiders) (Barnett & Cowan, 1976; Cowan, 1983). As was the case in our monkeys this avoidance behaviour in rats was found when a novel

object was presented in a familiar environment (Barnett, 1975; Barnett & Cowan, 1976). In a totally novel environment rats did not avoid novel objects.

The cause of the neophobia in our monkeys seems to be differ from that of the neophobia in Barnett's rats. According to Barnett (1975) the neophobic reaction in rats is a result of selection due to (human) pest control. Rats avoiding novelty (traps) survived longer and got more offspring than rats that did not avoid novelty. Whereas in rats avoidance of novelty was enhanced by selection (nature), in our monkeys the chance to develop a phobia was enhanced by growing up with a surrogate mother (nurture). This implies that factors other than selection can enhance the appearance of neophobic reactions.

Röder's found that most surrogate reared monkeys became neophobic. This raises the question about relevant differences between both rearing conditions. The surrogates were static whereas the mothers carried their infants about in the environment. There was a difference in the social context as well. In the surrogate condition only peers were available whereas in the mother condition next to peers other adult conspecifics were present.

In order to study the effects of the mobility of the mother, females were restrained in their radius of action by placing them in a small part of the cage which they shared with the harem-group they belonged to. Infants of these mothers were allowed to leave the separation cage and enter the cage of the harem-group.

In order to study the effects of the absence of other adults, females were restrained in their radius of action by confining them to a small part of the living-cage in which no other adult monkeys were present accept other restrained mothers. As in the harem condition the infants were allowed to enter the living-cage.

In addition to the study of the effects of these housing conditions of the mothers on their infants' reaction towards big novel objects, it was studied (in the harems) whether restraining the mothers had an effect on their behaviour. In the harem as well as in the condition in which no other adults were present it was studied whether the behavioural development and the development of the range of action of the infants was affected.

Maternal behaviour can have an effect on explorative behaviour of the offspring (Fairbanks & McGuire, 1988); in studies of Castell & Wilson (1971), Wolfheim et al. (1970) and Kaplan (1972) it was found that individual housing of a mother-infant dyad induced an increase in maternal rejection and avoidance behaviour. We therefore assessed whether the restriction, imposed upon the mothers of the experimental group (mothers that were restrained in their radius of action to a small part of the harem cage), had an impact on maternal behaviour of these mothers (chapter 3). It appeared that restrained mothers did not differ in their maternal behaviour (restriction, rejection, etc.) from mothers that were not restrained in their radius of action.

According to Kaplan (1972), the rejection by the mother of her infant was due to the increase of the number of contacts made by the infant towards its mother (see also Rosenblum, 1971). This increase occurred because for the infant the mother was the only individual to make contact with. In our setup however young of restrained mothers had the opportunity to leave the separation cage of their mothers and young of unrestrained mothers could enter it. This freedom of movement gave young of restrained mothers enough opportunity to make social contacts with other conspecifics and prevented these young from making more contacts with their mothers than young of unrestrained mothers. Further, our restrained mothers had, in contrast with Kaplan's subjects, a companion in the separation cage, and the width of the netting allowed the restrained mothers to make contact with conspecifics outside the separation cage. These opportunities for social interactions could have played a part in the finding that restrained mothers did not differ from unrestrained mothers in maternal behaviour.

Concerning the development of radius of action of young (chapter 4) there was a clear difference between infants of restrained mothers and infants of unrestrained mothers. During the first half year young of mothers of a harem group that were restrained in their radius of action stayed more within the proximity of their mothers than young of unrestrained mothers. During the second part of the year young of restrained mothers showed an increase in their development of radius of action and at the end of the first year these young hardly differed from young of unrestrained mothers.

According to Hinde & Spencer-Booth (1968), Hinde (1983), and Altmann (1980)

the development of the distance between mother and infant is strongly influenced by rejective and restrictive behaviour of the mother. In our setup however, restrained mothers did not differ in these maternal behaviours from unrestrained mothers; in the same period the distance between young and their unrestrained mothers was greater than the distance between young and their restrained mothers. It seems that next to age of the young, species (see Higley & Suomi, 1986), and environmental factors (Johnson & Southwick, 1987), the radius of action of the mother plays a part in the development of the distance between mother and infant. Our study, the studies of Johnson & Southwick (1987), and the findings of Higley & Suomi (1986) seem to confirm the opinion of Chalmers (1972) and Welker & Witt (1982) that maternal behaviour does not play a dominant role in the distance between mother and her infant.

The assumption of Hinde & Spencer-Booth (1968) and Berman (1980) that during the first 2-3 months young monkeys take the initiative in increasing the distance between themselves and their mothers seems to be confined to certain conditions. Whether young take the initiative to leave their mothers, apparently is dependent on the degree of familiarity of the environment. In contrast with young of restrained mothers, young of unrestrained mothers were familiar with the environment because they had been carried about in the environment by their mothers.

The presence of other adults (harem) seems to influence the development of the youngs' radius of action (chapter 6). Though young that grew up with restrained mothers without other adults left their mothers' separation cages already at an early age, they hardly enlarged their radius of action thereafter. Especially during the second part of the first year their radius of action did not increase, whereas, young of restrained mothers within a harem in this period considerably enlarged their radius of action.

These differences in the development of radius of action seem to confirm the hypothesis of Rosenblum (1971). He suggested that a complex environment (as created by the presence of other adult conspecifics) is aversive for young infants but becomes attractive when they grow older. The retardation of radius of action of young of restrained mothers within a harem could have been a consequence of a complex environment (movements, reactivity, and size of the conspecifics) which had to be entered without the

mother. When the young grew up the harem became attractive, leading to an enlargement of their radius of action. In the condition without other adults young stayed near their mothers' separation cages in the rear part of the cage. It seems that young monkeys do not move far away from their mothers to visit places where there are no other conspecifics.

We now return to the question whether maternal mobility and the absence of other adult monkeys have an effect on infants' reactions towards big novel objects.
When we compare the groups with respect to reactions to big novel objects it appears that being carried about in the environment by the mother during early infancy did not influence the subjects' ability to approach novel objects during individual tests at a later age (chapter 5). Growing up with restrained mothers within a harem group did not influence subjects' reactions towards big novel objects. Duijghuisen et al. (in prep) who compared a group of monkeys growing up with fixed surrogates with a group of monkeys growing up with mobile surrogates did not found differences between both groups in their reactions towards big novel objects. The phobic reactions towards big novel objects, that were found in surrogate-reared monkeys (Röder, 1990), apparently are not a consequence of the fact that surrogate-reared monkeys could not get acquainted with the environment by being carried about.

Growing up with restrained mothers but without other adults seemed to have little effect on the subjects' reactions to a big novel object (chapter 6). However, it appeared that these young hardly took pieces of apple when they were separated from their mothers and/or peers. This reservedness was not observed in young growing up in a harem. The cause of this reservedness could be that young growing up without a harem are more upset when separated than young that grow up in a harem. In a review Mineka & Suomi (1978) mentioned, among other things, three possible causes of severe reactions to separation. First, insecurely attached young generally spend less time away from their mothers and are more upset when separated from their mothers than securely attached young. A second explanation mentioned by Mineka & Suomi why young reared in a harem are less upset when separated than young reared without a harem is that harem-reared young are more socially sophisticated. According to Mineka & Suomi socially sophisticated young are less susceptible to separation induced despair than are monkeys raised in more restricted social

environments. This explanation is based upon the view that monkeys reared in a socially enriched environment have more experience in controlling their environment. Thirdly, unfamiliarity can enhance reactions to separation. In our study young reared with restrained mothers without other adults hardly visited the front part of the cage where the tests with a big novel object took place.

The outcome of the preliminary study with young that were reared with a restrained mother without a harem (retardation in development of radius of action and severe reactions to separation) is interesting enough to repeat the experiment.

In vervet monkeys a negative correlation was found between restrictive behaviour of the mothers and the willingness of their infants to enter a novel cage (Fairbanks & McGuire, 1988). In order to determine whether in our monkeys there was a relation between maternal behaviour and the reactions of young towards big novel objects, it was examined whether there was a relation between restrictive and rejective behaviour of the mother during the first half year of life of her infant and the reactions of the young towards big novel objects. Neither in both rearing conditions separately nor in all subjects together a correlation was found. Further it was examined whether young of extremely rejective and/or restrictive mothers, and young of mothers that hardly showed these behaviours differed in the number of sessions needed to approach the novel object. No difference was found too. Also the percentage of the time "off mother" young were beyond arms' reach of their mothers, and the age at which young approached a novel object for the first time, were not related.

Our results are in contrast with the findings of Fairbanks & McGuire (1988). However, it should be kept in mind that there are some procedural differences between the Fairbanks & McGuire study and our study. Fairbanks & McGuire tested the reactions to a novel cage without separating the subject from its group, whereas we tested the reaction to a novel object during separation.

In conclusion, it appeared that being carried about is not a prerequisite for the behavioural development of the infant; neither for the development of its radius of action (although retarded), nor for the development of its exploration of big novel objects. The

answer to the question whether mobility of the mother plays a role in the acquisition of phobic behaviour, as found by Röder in surrogate reared monkeys, is that this characteristic of the mother has no effect on the acquisition of phobic behaviour.

We return to the question what difference between a natural mother and a surrogate mother may be the cause of the phenomenon that most monkeys reared with surrogates become phobic.

Baldwin & Baldwin (1977, 1978) theorized about the development of exploration and play in young monkeys in terms of a sensory input zone in which a subject can function optimally. In this model the development of a young is related to the (non)social environmental conditions and the availability of the mother. To the mother arousal reducing qualities are granted that enable the young to approach arousal inducing stimuli. These qualities of the mother are unified by Bowlby in the term "secure base". The secure base model of Bowlby (see Bowlby, 1988) is commonly accepted as a useful starting point to analyse the development of a young primate (see Mineka & Suomi, 1978; Kraemer, 1992). In this view it is supposed that stimuli that cause an "overarousal" can be approached because the mother decreases the arousal level of her young to an optimal arousal level (see Baldwin & Baldwin, 1977; 1978; see also Bishof, 1975; Bronson, 1968; King, 1966; Rosenblum, 1971). According to Baldwin & Baldwin the capacity of an attachment figure to reduce arousal affects the young's ability to cope with arousal inducing stimuli. The arousal reducing qualities of the mother are a precondition for a development during which a young can get familiar with the environment. The better this arousal level develops the more a young is able to cope with arousal inducing stimuli encountered later.

It is not clear to what extent a natural mother and a surrogate mother differ in their quality as a secure base; the concept of "arousal" and "secure base" are difficult to quantify. Some authors consider the surrogate mother to be an adequate substitute of the natural mother (Mason & Capitanio, 1988). Others conclude that a surrogate mother is less secure than the natural mother, because surrogate-reared young respond to separation differently from young reared by natural mothers (Hennessy & Kaplan, 1982; Hennessy et al., 1979; Meyer et al., 1975; see also Reite, 1987). Whether an eventual difference in

arousal reducing qualities of the particular attachment figures is responsible for the difference in avoidance behaviour between surrogate- and mother-reared subjects is unclear till now.

Another possible factor of influence is that, in contrast to surrogates, mothers are responsive. It could be of importance for a young to be directed by its attachment figure. Maternal behaviours like rejection and restriction seem to influence young's development. In what way these maternal behaviours play a role in the development of explorative behaviour is partly known. Up till now maternal behaviour mainly was studied by looking at the effect of differences in quantity of restriction and rejection on the part of the mother upon the development of independence of the young (e.g. Altmann, 1980; Berman, 1980; Hinde, 1983; Simpson et al., 1986). The question whether the absence of these maternal behaviours, as in surrogates, has an effect on young, has not been answered yet. Studies of Rosenblum & Pauly (1984) and Andrews & Rosenblum (1991) indicate that there may be an effect of the quantity of maternal attention. These authors found that reduced maternal attention causes an increase of disturbed behaviour and has a negative effect on exploration of novelty in young.

The last aspect to be discussed here is the availability of conspecifics other than the mother. In the model of Baldwin & Baldwin (1977; 1978) next to the mother another variable can play a part, namely the presence of arousal inducing stimuli. If we consider the presence of other adults as a source of environmental stimulation, it appears that at first this stimulation retards and at a later age stimulates the development of the radius of action in young monkeys. Environmental enrichment enhances infant's independence (see Jensen et al., 1968). In rats it was found that environmental enrichment affects the exploration of novel objects. Compared to rats that were living in a impoverished environment, rats that were exposed to an enriched environment for 2 hours daily, spent more time in exploration of novel objects and also showed a greater diversity in their exploration (Widman & Rosellini, 1990).

In view of the results obtained by studying young that grew up with a restrained mother without a harem, the question to be asked here is to what extent the absence of other adults in the surrogate condition, as it was used by Röder, differs in social stimulation from the mother condition (harem) and to what extent this difference has an effect on

avoidance of big novel objects.

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Summary

Summary

In a series of studies it was found that rearing condition plays an important role in the acquisition of phobic behaviour in long-tailed macaques (*Macaca fascicularis*) (Röder, E.L. 1990, Rearing condition and the acquisition of phobic behaviour in monkeys. Dissertation, Nijmegen: Benda BV). Röder found that most monkeys reared with surrogate mothers in a peer group avoided a big novel object (a paper bag), whereas most monkeys reared by their own mothers in a harem approached that object. The avoidance of the bag persisted up into adulthood. This persistent avoidance of a clearly harmless object was qualified as phobic behaviour. The avoidance behaviour of these monkeys can serve as an animal model of human phobia: also human phobics persistently avoid harmless objects or situations.

Several theories concerning the origin of phobias have been studied experimentally. The most current view is that phobias are acquired through the association of an object or a situation with an aversive or frightening experience (aversive conditioning). The evidence for this view stems from experiments with rats. There also is a theory assuming that objects or situations that endangered life during phylogeny become an object of phobia much easier than other stimuli (preparedness theory). According to a third theory one can develop a phobia as a consequence of observing conspecifics reacting fearfully to a certain event or a certain object (observation learning). The evidence for the preparedness theory as well as for observation learning stems from experiments with rhesus monkeys.

The animal model presented by Röder in three respects clearly differs from the animal models just mentioned. In contrast to what is usual in these animal models, in the model presented by Röder: -a harmless object was avoided, -no aversive conditioning was applied, -the monkeys could not see conspecifics reacting fearfully to the object. However, the model does correspond with theories in which it is assumed that certain early experiences can affect the development of fearful behaviour later in life.

This thesis deals with two main questions concerning the phobic behaviour in long-tailed macaques; -1 what are the characteristics of the phobic behaviour described by Röder, and, -2 what is the relevant difference between surrogate-rearing and mother-

rearing with respect to the development of phobic behaviour in monkeys reared with surrogate mothers.

Concerning the characteristics of phobic behaviour the question was whether avoidance behaviour was restricted to the particular object Röder used (the paper bag) or that other objects would be avoided as well. This question was put as it was not clear whether the bag contained stimuli causing the monkeys to avoid it.

Therefore monkeys, which were known to have avoided or approached the bag, successively were exposed to the bag, to two other big novel objects, and to four small novel objects. It appeared that monkeys that avoided the bag (called phobic monkeys) also avoided the other big novel objects. Monkeys that approached the bag (called non-phobic monkeys) also approached the other big novel objects. The small novel objects were approached by phobic as well as by non-phobic monkeys. So in phobic monkeys the size of the object determined their reaction towards the object.

The characteristics of the phobic behaviour again came up in another experiment. Instead of successive presentations of novel objects to the same subjects, like in the previous experiment, this time one group of monkeys was tested with the bag and another group with a chair-like construction of the same size as the bag. Again it appeared that the shape of the object did not determine whether the objects were approached or avoided.

Whether the age at which a subject was exposed to a big novel object for the first time played a role in its reaction towards that object was studied by confronting the same monkeys from the preceding experiment with another, second, big novel object at a later age. It appeared that there was no difference between reactions towards the first and the second object.

We found that phobic as well as non-phobic subjects approached small novel objects. Further it appeared that neither the shape of the big novel object nor the age at which a subject was confronted with the object for the first time, had an effect on the subjects' reaction. This leads us to the conclusion that we are dealing with a neophobia of big objects.

The study concerning the question which difference between surrogate-rearing and

mother-rearing was responsible for the finding that most surrogate reared monkeys became neophobic was aimed mainly at the fact that, in contrast to surrogates, mothers are mobile and carry their infants about in the environment. Further attention was paid to the difference in social stimulation between the surrogate-rearing and the mother-rearing condition.

Mobility of the mother could be an important factor in the development of the infant. Whether it likes it or not the infant is brought in touch with all kinds of environmental stimuli (physical as well as social) with the mother. It is assumed that the proximity of the mother reduces the infant's fear evoked by novelty. Probably this process stimulates the development of the infant's explorative behaviour. In the surrogate condition the infant is not carried about in the environment and when it becomes upset there is no mother nearby to calm it down. This situation could impede the development of explorative behaviour and as a consequence surrogate-reared monkeys could be more reluctant than mother-reared monkeys to approach big novel objects.

In order to find out whether "mobility" of the mother has an effect on the development of explorative behaviour, mothers were restrained to a small part of the cage of the harem they belonged to. This so called separation cage was provided with a slit in the netting through which young, but not adult monkeys could pass. Young of mothers in separation cages, like young reared with surrogates, lacked their mothers' escort during excursions in the environment. In the same harem cage there were infants with mothers freely moving around. These infants formed the control group.

In the study by Röder another difference between surrogate-rearing and mother-rearing was that in the surrogate condition only peers were present, whereas, in the mother condition peers as well as (sub)adults were present.

In a preliminary study attention was paid to the question whether the composition of the group plays a role in the development of phobic behaviour. Like in the study of the effects of the "mobility" of the mother, mothers kept in a separation cage and their infants could freely move in and out this cage. Outside the separation cages there only were peers.

Besides effects on the development of explorative behaviour, restraining of the mother could affect the mother-infant relationship. Therefore also attention was paid to the

mother-infant relationship during the first half year. The development of explorative behaviour and the range of action of the infant was studied during one year.
No differences in maternal behaviour between restrained mothers and unrestrained mothers were found. However, during the first half year infants of restrained mothers kept closer to their mothers than infants of unrestrained mothers. During the second part of the first year the infants of restrained mothers showed an increase in their range of action and at the end of the first year they hardly differed from infants of unrestrained mothers. Further it appeared that infants of restrained mothers did not differ from infants of unrestrained mothers, in the development of exploration, locomotion, social- and autoactive-behaviour.
The behavioural development of infants that grew up with restrained mothers and peers, at first resembles the development of subjects that grew up with restrained mothers in a harem. The development of their range of action was retarded, but in contrast to subjects that grew up with restrained mothers in a harem, they did not enlarge their range of action in the course of the second half year. During the first year of life these subjects mainly stayed within proximity of the separation cages in which their mothers were housed.

Concerning the effects of restraining the mother on infant's reaction towards big novel objects it appeared that growing up with a restrained mother did not affect the reaction towards a big novel object. Infants of restrained mothers did not differ from infants of unrestrained mothers in their reactions towards the novel object. Like in the study of Röder most mother reared subjects approached the big novel object.
The effect of growing up with restrained mothers and peers was twofold. Half the number of subjects avoided the bag whereas the others approached the object. Because these subjects also seemed to be affected by separation, in a way that it inhibited their explorative behaviour, the results of this pilot study do not allow us to draw decisive conclusions about the effects of the absence of adults on reactions towards big novel objects.

According to the literature about mothering-styles rejective and protective behaviour of the mother can affect the development of explorative behaviour in young monkeys. In our subjects, however, no relation was found between the reaction to a big

novel object and rejective and protective behaviour of the mothers. Even young of extremely rejective or protective mothers did not significantly differ from each other concerning behaviour towards a big novel object.

Duijghuisen compared the development of behaviour and the reaction to big novel objects in monkeys that grew up with stationary or with mobile surrogate mothers (Duijghuisen, J.A.H., Thesis in prep.). In agreement with our findings Duijghuisen found that "mobility" of the surrogate at first did affect the range of action of the infant monkeys but had no influence on avoiding or approaching big novel objects.

So it seems that "mobility" of the mother is not crucial for the development of the capacity of the infant to approach big novel objects.

It is concluded that:

-the avoidance of big novel objects can be considered a neophobia;

-restraining the mother in a small cage inside the cage of her harem-group has no effect on the mother-infant relationship;

-restraining the mother retards the development of infant's radius of action but being carried about by the mother is not a prerequisite for the development of infant's independence;

-restraining the mother does not affect infant's capability to explore big novel objects;

-growing up with a restrained mother and with peers but without free-moving (sub) adult conspecifics retards the development of infant's radius of action but seems to have little effects on the infants ability to explore big novel objects during individual exploration tests.

The question which difference between surrogate-rearing and mother-rearing is responsible for the finding that most surrogate-reared monkeys avoided a big novel object, remains unanswered.

It is suggested that further studies pay attention to;

-whether a surrogate mother and a natural mother differ in functioning as a secure base,

and whether differences in security are related to differences in approach-avoidance behaviour with respect to big novel objects,

-whether the enrichment of an environment, in which a young grows up, has an effect on young's capability to explore big novel objects.

Samenvatting

Samenvatting

Uit het onderzoek van Röder (Röder, E.L., 1990, *Rearing condition and the acquisition of phobic behaviour in monkeys*, Benda BV, Nijmegen) kwam naar voren dat de opgroeiconditie een belangrijke rol speelt bij het ontstaan van fobisch gedrag bij Java-apen (*Macaca fascicularis*). Röder vond dat de meeste apen die samen met leeftijdsgenootjes bij een kunstmoeder opgroeiden een groot nieuw voorwerp (een grote papieren zak) vermeden terwijl de meeste apen die bij hun moeder in een harem groep opgroeiden dit voorwerp benaderden. Apen die op jonge leeftijd de zak vermeden, bleken toen ze volwassen waren, dit voorwerp nog steeds te vermijden. Dit persistente vermijden van een volstrekt ongevaarlijk voorwerp werd gekwalificeerd als fobisch gedrag. Het vermijdingsgedrag van deze apen kan als model dienen voor fobieën bij de mens omdat persistente vermijding van ongevaarlijke voorwerpen of situaties een essentieel kenmerk is van door mensen vertoonde fobieën.

Diverse theorieën omtrent het ontstaan van fobieën werden dierexperimenteel getoetst. De meest gangbare opvatting is dat een voorwerp of situatie object van een fobie kan worden indien dit voorwerp of deze situatie wordt geassocieerd met een onaangename of beangstigende gebeurtenis (aversieve conditionering). Deze opvatting is grotendeels gebaseerd op experimenteel onderzoek aan ratten. Naast deze theorie is er een theorie die veronderstelt dat voorwerpen of situaties die in het verre verleden van de soort levensbedreigend waren, veel gemakkelijker object van een fobie worden dan andere zaken (de "preparedness" theorie). Volgens een derde theorie kan men een fobie ontwikkelen als gevolg van het waarnemen van soortgenoten die angstig reageren op een bepaalde gebeurtenis of een bepaald voorwerp (observatie leren). Zowel voor de theorie van observatie leren als voor de preparedness theorie stonden rhesus apen model.

Het door Röder gepresenteerde model wijkt in drie opzichten duidelijk af van de zojuist genoemde modellen. In tegenstelling tot wat gebruikelijk is in deze diermodellen werd: -1 een ongevaarlijk voorwerp vermeden, -2 geen aversieve conditionering toegepast, en -3 de reactie van soortgenoten op het voorwerp niet getoond. Het model van Röder sluit wel aan bij theorieën waarin wordt gesteld dat bepaalde ervaringen tijdens het opgroeien van invloed kunnen zijn op angstig gedrag op latere leeftijd.

Dit proefschrift gaat in op twee vragen: -1 wat is de aard van het fobische gedrag dat Röder beschreef, -2 welk verschil tussen het opgroeien bij een kunstmoeder en het opgroeien bij een moeder is verantwoordelijk voor het ontstaan van fobisch gedrag zoals dat werd gevonden bij apen die bij kunstmoeders opgroeiden.

Wat de aard van het fobisch gedrag betreft, werd de vraag gesteld of het vermijdingsgedrag van de apen beperkt was tot een bepaald voorwerp (de zak), of dat andere, hun onbekende, voorwerpen ook zouden worden vermeden. Deze vraag werd gesteld omdat het niet duidelijk was of de zak eigenschappen had die de apen aanleiding gaven tot vermijding. Om deze vraag te beantwoorden werden de apen uit het onderzoek van Röder successievelijk hertest met de zak, en getest met twee onbekende voorwerpen van gelijke grootte als de zak (een driehoek en een stoel), en met vier kleine onbekende voorwerpen. Het bleek dat apen die de zak vermeden (fobische apen genoemd) ook de driehoek en de stoel vermeden en dat apen die de zak benaderden (niet fobische apen genoemd) ook de driehoek en de stoel benaderden. De kleine voorwerpen werden door zowel fobische als niet fobische apen benaderd. Bij fobische apen bleek dus de afmeting van het voorwerp bepalend voor hun reactie.

De aard van het fobische gedrag kwam in een ander experiment opnieuw aan de orde. In plaats van successieve aanbieding van enkele grote onbekende voorwerpen bij dezelfde apen, werd een groep apen enkele malen met de zak en een andere groep apen enkele malen met de stoel getest. Uit deze testen bleek wederom dat de vorm niet van invloed was op het al dan niet vermijden van de voorwerpen.

Of de leeftijd waarop een aap voor het eerst met een groot onbekend voorwerp wordt geconfronteerd van invloed is op het al dan niet vermijden van dat voorwerp werd onderzocht door beide zoëven genoemde groepen apen op een latere leeftijd elk met een tweede onbekend voorwerp te testen. Er werd geen verschil gevonden tussen de reacties op het eerste en het tweede voorwerp.

Het gegeven dat kleine onbekende voorwerpen door zowel fobische als niet fobische apen werden benaderd en dat noch de leeftijd waarop een aap voor het eerst met een groot voorwerp werd geconfronteerd noch de vorm van het voorwerp van invloed was op het al dan niet vermijden van dat voorwerp, duidt erop dat het vermijdingsgedrag van de apen gebaseerd is op een neofobie voor grote voorwerpen.

Het onderzoek betreffende de vraag welk verschil tussen de kunstmoeder-conditie en de moeder-conditie ten grondslag ligt aan de bevinding dat de meeste bij een kunstmoeder opgegroeide apen neofobisch waren, richtte zich voornamelijk op het gegeven dat, in tegenstelling tot kunstmoeders, natuurlijke moeders mobiel zijn en hun jongen met zich mee dragen. Op deze wijze komt een jong, of het wil of niet, in de nabijheid van de moeder met allerlei zaken in de omgeving in aanraking. Dit zou de ontwikkeling van het exploratief gedrag van het jong positief kunnen beïnvloeden. Men neemt aan dat voor een jong dat angstig is voor onbekende zaken de nabijheid van de moeder kalmerend werkt. In de kunstmoeder-conditie wordt het jong niet naar onbekende zaken gebracht, noch wordt het gekalmeerd. De ontwikkeling van exploratief gedrag zou aldus achter kunnen blijven, met als gevolg dat het jong onbekende voorwerpen vermijdt.

In het kader van het onderzoek naar het effect van de "mobiliteit" van de moeder op de ontwikkeling van exploratief gedrag bij het jong werden apinnen direct na de geboorte van hun jongen opgesloten in een klein gedeelte van de leefruimte van de haremgroep waartoe zij behoorden. Deze separatiekooi was voorzien van een opening waar wel jonge maar geen volwassen apen door konden. Jongen van moeders in separatiekooien misten, evenals jongen die bij een kunstmoeder opgroeiden, begeleiding bij hun excursies in de leefruimte.

In het onderzoek van Röder bestond een tweede verschil tussen de kunstmoeder-conditie en de moeder-conditie hieruit dat in de kunstmoeder-conditie alleen leeftijdsgenootjes aanwezig waren en in de moeder-conditie naast leeftijdsgenootjes ook oudere soortgenoten. In een verkennend onderzoek werd onderzocht of de samenstelling van de groep waarin een jong opgroeit een rol speelt in het vermijden van grote onbekende voorwerpen. Evenals in het onderzoek naar de invloed van de "mobiliteit" van de moeder werden de moeders beperkt tot een klein gedeelte van de leefruimte en konden de jongen de separatiekooi vrij in en uit gaan. Buiten de separatiekooien bevonden zich alleen maar leeftijdsgenootjes.

Omdat het niet uitgesloten was dat het beperken van de bewegingsvrijheid van de moeder invloed zou hebben op de moeder-kind relatie, werd tijdens het eerste halve jaar ook aandacht besteed aan deze relatie. De ontwikkeling van het exploratief gedrag en van

de actieradius van het jong werd gedurende één jaar gevolgd.

Het bleek dat moeders die al dan niet in hun bewegingsvrijheid waren beperkt niet verschilden in moederlijk gedrag. Jongen van in hun bewegingsvrijheid beperkte moeders verschilden niet in de ontwikkeling van exploratief gedrag van jongen van moeders wier bewegingsvrijheid niet was beperkt. Wel was er een verschil in ontwikkeling van de actieradius. Jongen van "beperkte" moeders bleven gedurende het eerste half jaar meer in de nabijheid van hun moeders dan jongen van "onbeperkte" moeders. In het tweede half jaar vertoonden ze echter een sterke toename in hun actieradius en na 1 jaar verschilden ze nauwelijks meer van jongen van "onbeperkte" moeders.

De jonge apen die opgroeiden bij "beperkte" moeders en bij leeftijdsgenootjes bleven ook achter in de ontwikkeling van hun actieradius. Gedurende hun eerste levensjaar bleven ze voornamelijk in de nabijheid van hun moeders in de separatie-kooien. Wat het gebruik van de leefruimte betreft leek het erop dat deze jongen niet op plaatsen kwamen waar zich geen andere soortgenoten bevonden.

Jongen opgegroeid bij "beperkte" moeders verschilden niet van jongen opgegroeid bij "onbeperkte" moeders wanneer ze werden getest met een groot onbekend voorwerp. Evenals bij Röder, benaderden de meeste bij moeders opgegroeide apen grote onbekende voorwerpen.

Jongen die opgroeiden bij beperkte moeders en met alleen leeftijdsgenootjes bleken wanneer ze met een groot nieuw voorwerp werden geconfronteerd, hiermee meer moeite te hebben. Van de zes apen benaderden er drie het voorwerp. Dat deze apen, evenals de apen die bij een surrogaat moeder opgroeiden, fobisch waren, kon niet worden geconcludeerd. Dit omdat deze apen zeer aangedaan waren door scheiding van soortgenoten gedurende de exploratie testen.

De literatuur vermeldt dat moederlijk gedrag, in termen van afwijzen en beperken, van invloed kan zijn op de ontwikkeling van het exploratieve gedrag van het jong. Daarom werd zowel voor beide opgroeicondities apart als voor alle apen tezamen bekeken of er een relatie bestond tussen de reacties van het jong op een groot onbekend voorwerp enerzijds en het afwijzend en beperkend gedrag van de moeder anderzijds. Er bleek echter

bij onze apen geen relatie te bestaan tussen moederlijk gedrag en de reacties op een onbekend object. Ook jongen van extreem afwijzende of beperkende moeders weken niet duidelijk van elkaar af in gedrag ten aanzien van een groot onbekend voorwerp.

Duijghuisen vergeleek de ontwikkeling van het gedrag en de reactie op grote onbekende voorwerpen bij apen die opgroeiden bij gefixeerde of bij mobiele kunstmoeders (Duijghuisen, J.A.H., proefschrift in voorbereiding). In overeenstemming met mijn resultaten vond Duijghuisen dat "mobiliteit" van de kunstmoeder aanvankelijk wel van invloed was op de actieradius van het jong maar niet op het al dan niet vermijden van grote onbekende voorwerpen. Evenals bij Röder vermeden de meeste bij kunstmoeders opgegroeide apen de grote onbekende voorwerpen.

Het verschil tussen jongen die bij kunstmoeders opgroeiden en jongen die bij hun moeders opgroeiden in vermijding van grote nieuwe voorwerpen, zoals door Röder gevonden, blijkt dus niet veroorzaakt door het verschil in "mobiliteit" van de hechtingsfiguren (statische kunstmoeder versus mobiele moeder).

Geconcludeerd wordt dat:

-het vermijdingsgedrag ten aanzien van grote nieuwe objecten kan worden beschouwd als een neofobie;

-het beperken van de bewegingsvrijheid van de moeder binnen een harem groep geen effect heeft op de moeder-kind relatie;

-het beperken van de moeder de ontwikkeling van de actieradius van haar jong vertraagt, maar het rond gedragen worden door de moeder geen voorwaarde is voor de ontwikkeling van de onafhankelijkheid van het jong;

-het beperken van de moeder geen effect heeft op het gedrag van het jong wanneer het met grote nieuwe objecten wordt geconfronteerd;

-het opgroeien met beperkte moeders en leeftijdsgenootjes maar zonder andere volwassen apen de ontwikkeling van de actieradius van het jong vertraagt en maar weinig effect lijkt te hebben op het vermogen van het jong om gedurende individuele testen grote nieuwe voorwerpen te exploreren.

De vraag welk verschil tussen de kunstmoeder-conditie en de moeder-conditie ten grondslag ligt aan de bevinding dat de meeste bij een kunstmoeder opgegroeide apen grote nieuwe objecten vermijden is dus niet beantwoord.

Verder onderzoek dient in te gaan op de vraag of:

- voor een jonge aap een surrogaat moeder en een natuurlijke moeder verschillen in het functioneren als een veilige basis, en of dit een rol speelt bij het al dan niet vermijden van grote onbekende objecten
- de stimulus rijkdom waarin een jonge aap opgroeit van invloed is op het al dan niet vermijden van grote onbekende objecten op latere leeftijd.

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In September 1987 ging ik naar Nijmegen om bij de vakgroep Vergelijkende en Fysiologische Psychologie onderzoek te doen aan de ontwikkeling van exploratief gedrag bij de Java-aap. Dit resulteerde in het voor u liggende proefschrift. Deze zou echter niet tot stand zijn gekomen zonder de medewerking van veel mensen.

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Curriculum vitae

Johan Vochteloo werd op 19 januari 1952 geboren te Groningen. Na de Analistenschool en de applicatiecursus Milieukunde aan de Rijkshogere Landbouwschool, begon hij in 1978 aan de studie Biologie aan de Rijksuniversiteit te Groningen. Tijdens zijn studie verrichtte hij onderzoek aan de broedbiologie van de torenvalk (o.l.v. Dr. S. Daan), de paarband bij de zwarte kraai (o.l.v. Dr. I. Bossema), en agressief gedrag bij de rat (o.l.v. Dr. J.M. Koolhaas). In 1987 trad hij in dienst van de Katholieke Universiteit te Nijmegen als assistent in opleiding bij de vakgroep Vergelijkende en Fysiologische Psychologie o.l.v. Prof. Dr. J.M.H. Vossen. Hier onderzocht hij, onder begeleiding van Dr. P.J.A. Timmermans, het effect van de actieradius van de moeder op de ontwikkeling van exploratief gedrag van haar jong bij de Java-aap. Dit resulteerde in dit proefschrift.